‘You scratch my back and I scratch yours’ versus ‘Love thy neighbour’

Two proximate mechanisms of reciprocal altruism

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RIJKSUNIVERSITEIT GRONINGEN

'YOU SCRATCH MY BACK AND I SCRATCH YOURS' VERSUS 'LOVE THY NEIGHBOUR'.

TWO PROXIMATE MECHANISMS OF RECIPROCAL ALTRUISM

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Rita Caterina Smaniotto
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Promotores:
Prof. dr. F.N. Stokman
Prof. dr. A.P. Buunk
Copromotores:
Dr. H. de Vos
Dr. A. Flache

Beoordelingscommissie:
Prof. dr. P.A.M. van Lange
Prof. dr. S. Lindenberg
Prof. dr. F.B.M. de Waal

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CHAPTER 1

Introduction

1 Introduction

Imagine that a close friend comes to you and confides that he is in financial trouble because of some misfortune beyond his control; for example, his wallet had been stolen. What would you do should he ask you to lend him some money? If you had sufficient funds in your bank account, you would probably grant his request. How would you react, however, if he should come to you a few days later and asks you to drive him to the police station to report the theft? And what would you do if he should ask you for an additional loan three weeks thereafter, as it was still impossible to access his bank account? You would probably be torn between two considerations or perspectives. On the one hand, your friend's requests for favors might cause you to become irritated and indignant, since he has not repaid his debts. On the other hand, you care for your friend and want to help him. I refer to the first perspective as "scorekeeping," as it considers primarily the balance between benefits provided and benefits received. I refer to the second perspective as "bonding," as it focuses on the needs of the other person. In this case, should the scorekeeping perspective prevail, you would probably refuse to grant your friend's latest request. In contrast, should the bonding perspective prevail, you will probably help him again.

This dissertation focuses on these two perspectives. I will use evolutionary psychological arguments to provide a theoretical background for the scorekeeping

and bonding perspectives, and derive hypotheses about their occurrence. Evolutionary psychology considers these perspectives to be rules or heuristics that have evolved to cope with recurrent situations that our ancestors encountered. Such rules or heuristics are called *proximate mechanisms*, as they describe *how* people behave in particular domains of social life. However, when applying an evolutionary framework, proximate mechanisms cannot be studied in isolation from the question of *why* they evolved among our ancestors. In other words, what were the benefits of these proximate mechanisms to the survival and reproduction of individuals (i.e., an individual's fitness)? The answer to this question provides the *ultimate cause* of these mechanisms. According to evolutionary psychology, the fitness benefit, or ultimate cause of helping or doing favors for another unrelated individual boils down to *reciprocal altruism*: helping another individual can be beneficial if that individual reciprocates in the future.

Most evolutionary psychologists consider scorekeeping to be the primary mechanism of reciprocal altruism. The reason is that individuals who accept help but never return anything are better off in terms of fitness than are individuals who provide unconditional help. Therefore, a mechanism has evolved that leads us to keep track of benefits provided and benefits received and to avoid help individuals who do not repay their debts.

Recently, however, several scholars have come to realize that scorekeeping mechanisms cannot explain all instances of reciprocal altruism and that another mechanism, such as bonding, might be at work. Moreover, taking the conditions of our evolutionary past into account, scorekeeping mechanisms may have even been detrimental to fitness. Yet, the concept of a bonding mechanism has not received much attention in evolutionary psychology.

The primary goal of this dissertation is therefore to demonstrate that the scorekeeping mechanism is not so ubiquitous as is generally believed and to show that there is considerable evidence for the operation of an additional mechanism. At some points I will go a step further, arguing that bonding is the primary mechanism of reciprocal altruism, whereas scorekeeping is a relatively recent cultural adaptation. Since emotions are considered to play an important role in the evolutionary psychological concept of proximate mechanisms, a third goal is to examine the effect of emotions on typical bonding and scorekeeping behavior. Data and findings from various sources will be used to address these issues. Chapter 2 is a critical review of anthropological studies on food sharing among hunter-gatherers. Chapter 3 deals with simulation data, and Chapters 4 and 5 present the results of scenario experiments.

The section to follow begins with a brief discussion of evolutionary psychology. It elaborates on the importance of the ancestral environment, the focus on proximate mechanisms, and the role of emotions in evolutionary psychology. The subsequent section introduces the concept of reciprocal altruism as an ultimate explanation for helping behavior and presents the scorekeeping and bonding mechanisms as alternative proximate mechanisms of reciprocal altruism. Section 4 discusses the merits of an evolutionary perspective for sociology, as well as some well-known criticisms of evolutionary approaches to human social behavior. The final section provides an overview of the dissertation.

2 Evolutionary psychology

Evolutionary psychology applies the theory of evolution to the domain of human behavior. Thus, it assumes 1) that behavior, or behavioral design, has a genetic basis, and 2) that during the course of evolution those behavioral designs have been selected that promoted the propagation of the genes responsible for those behavioral designs (Dawkins 1989). Moreover, evolutionary psychology makes two additional claims. First, our present behavioral designs are the result of selection pressures in *ancestral environments*. Second, adaptations take the form of *domain-specific psychological mechanisms*. The two sections to follow elaborate these assumptions.[1] Because emotions play an important role in the concept of psychological mechanisms, the third section discusses the role of emotions.

2.1 Assumption 1: Humans are adapted to ancestral conditions

2.1.1 The environment of evolutionary adaptedness

Evolutionary psychologists argue that it takes many generations for new traits to evolve and become part of a species' repertoire. Therefore, explanations of current behavior should consider ancestral conditions (e.g., Buss and Kendrick 1998; Crawford 1998; Durrant and Ellis 2003; Rossano 2003; Symons 1992; Tooby and Cosmides 1990b). Understanding any adaptation, regardless of whether it is a morphological or a behavioral design feature, requires consideration of the

[1] Although most evolutionary psychologists agree about these two assumptions, the extent to which various authors elaborate and emphasize them varies considerably. My primary focus is on the accounts provided by Leda Cosmides and John Tooby, whom many consider the founders of evolutionary psychology (Cosmides and Tooby 1992). In this discussion, therefore, "evolutionary psychology" refers to their representation.

environment in which the trait evolved, the *Environment of Evolutionary Adaptedness* (EEA) (Bowlby 1969). The EEA of a species does not refer to a specific place or time, as different traits or design features originated in different places and at different times. For example, the EEA of the design feature walking (on land) lies about 400 million years in the past, whereas the EEA of bipedality lies only about 5 million years ago. Tooby and Cosmides (1990b, p. 386) define the EEA for a species as "a statistical composite of the adaptation relevant properties of the ancestral environment encountered by the members of ancestral populations, weighted by their frequencies and fitness-consequences." For most purposes, however, the EEA for a species can be taken to refer to the most recent segment of a species' evolution, in which it took its present form and diverged from related species. For the human species, this is the Pleistocene era, the period between approximately 1.5 million and 10,000 years ago (Tooby and Cosmides 1990b). With some minor exceptions (e.g., intolerance for milk among some non-white populations [see McCracken 1971]), the post-Pleistocene period was too short to have resulted in any complex changes in behavioral or morphological design (Symons 1992, p. 138; Tooby and Cosmides 1989, p.34).

It should be emphasized that this does not mean that all of our characteristics were formed during the Pleistocene period. Many design and behavioral features originated much earlier and are shared with other species. Examples include our basic body plan, visual system, sexual reproduction patterns (including displays of coyness), and tendency to care for our offspring. Neither does it mean that the Pleistocene period was a featureless monolith in which life was simple and constant (e.g., see Turke [1990] for this criticism). As is evident from the wide geographical range in which human remains have been found and the occurrence of several strong climatic changes, humans did encounter various habitats and changes in environmental conditions during this period. What *was* constant, however, was their nomadic existence. Our ancestors lived as hunter-gatherers until the emergence of agriculture 10,000 years ago. Evolutionary psychology assumes that those living conditions have shaped our present behavioral design features.

2.1.2 Pleistocene selection pressures

Given that humans are adapted to Pleistocene conditions, it is important to know which selection pressures our ancestors encountered in this environment. This section provides a sketch of the Pleistocene selection pressures and how our ancestors changed from arboreal apes to highly social primates. This sketch is

unavoidably speculative. Although climatological, ecological, paleo-anthropological, and archaeological data support this portrayal, it remains impossible to go back in time and determine whether it actually happened this way.

Climatic changes at the end of the Miocene era reduced the range of tropical rain forests and increased the prevalence of savanna-like environments, which had become abundant as early as five million years ago. Compared to forest environments, resources in such environments are more spatially patchy, seasonally variable, and overall less abundant (Boehm 1999; Boyd and Silk 1997; Foley 1987; 1996; Folch and Camarasa 2000; Tooby and DeVore 1987). The open environment also made our ancestors more vulnerable to predators. Our ancestors, who had previously lived as tree-dwelling apes, were forced to adapt to the new environment. Phylogenetic comparisons of extant primates suggest that the social organization of our hominoid ancestors consisted of small groups ranging through the forest. Groups were centered on a number of kin-related males, whereas females dispersed to other groups at maturity (Di Fiore and Rendall 1994; Foley 1996; 2001; Rodseth et al. 1991).

What types of changes in social organization occurred when the habitat of these apes changed from rain forest to savanna? The literature on this subject provides several interconnected arguments. First, the patchy distribution of food resources (an important part of which consisted of large animals) and the presence of predators formed a selection pressure for increasing group size to extend beyond the boundaries of kinship (Boyd and Silk 1997; Hyland 1993; Tooby and DeVore 1979). Moreover, because individuals had to travel large distances to acquire food, groups tended to separate into smaller groups during the day, returning to the campsite to spend the night together (Barrett et al. 2002; Isaac 1978; Kummer 1971; Kurland and Beckerman 1985).

Social organization in the form of *fission-fusion groups* required individuals to maintain a full range of ties in the absence of spatial proximity, which was possible only in the presence of strong bonds (Foley 1996; Rodseth et al. 1991). The need to maintain a growing number of complex relationships subsequently selected for an increase in brain size (Dunbar 1993; Humphrey 1976). The increased dependence on meat may have played an important role in the expansion of the brain, because meat provides the body with more proteins and energy than do plant foods, and takes less energy to digest (Foley 1996; Tooby and DeVore 1979). In its turn, the increase in brain size selected for even higher levels of sociality because it led to earlier birth and a longer period of infant altriciality. Consequently, interdependence increased between group members, with females becoming particularly more dependent on males (Deacon 1997; Foley 1996).

Finally, food sharing was very adaptive within these interdependent groups living in harsh conditions, as it reduced the risk of starvation (Boyd and Silk 1997; Campbell 1979; Kurland and Beckerman 1985; Winterhalder 1986). Furthermore, the nature of the food sources, particularly meat, made the costs of sharing relatively low: captured animals usually provided more meat than one person could consume. The practical infeasibility of storage made sharing a sensible alternative (Boyd and Silk 1997; de Waal 1996; Tooby and DeVore 1979).

2.2 Assumption 2: Humans are equipped with domain-specific psychological mechanisms

The previous section argued that humans are adapted to the conditions of the Pleistocene environment. The evolutionary psychological view interprets adaptations as domain-specific mechanisms (Symons 1992; Tooby and Cosmides 1990b). Domain-specific mechanisms are activated by cues that consistently accompanied fitness-relevant situations in the EEA. Through a series of internal monitoring and communication systems, the appropriate perceptual, physiological, and behavioral responses are selected and activated. For example, the cue "large fanged animal approaching" triggers a whole array of physiological changes that prepare the individual to flee, or, if flight is not possible, to fight the animal. The internal cue "low blood sugar" urges the individual to find food and eat. Emotions play an important role in the link between cues and responses: the experience of fear compels an individual to flee; the experience of hunger compels an individual to find food and eat (see Section 2.3). In summary, evolutionary psychologists conceive of the mind (both the human and non-human mind) as a collection of domain-specific mechanisms, each evolved to cope with a specific fitness-relevant situation in the EEA. This is the meaning of the often used metaphor of the mind as a Swiss army-knife.

The focus on domain-specificity stands in contrast to an alternative view, which conceives of humans as fitness maximizers. According to this view (known variously as Darwinian anthropology, Darwinian social science, and sociobiology), an organism's behavior is not steered by domain-specific mechanisms, but by a general rule to do whatever promotes the individual's fitness. Rather than using knowledge about the ancestral environment to formulate domain-specific psychological mechanisms and make predictions about present behavior and

preferences, Darwinian anthropologists focus on the adaptive consequences of specific behaviors in the present environment.[2]

Most evolutionary psychologists consider the claim that organisms are fitness maximizers to be fundamentally wrong or, at the very least, highly susceptible to misinterpretation (Symons 1992; Tooby and Cosmides 1990b). If organisms are fitness maximizers, or if they behave *as if* they are maximizing fitness, then organisms must somehow be able to respond adaptively to any given situation. In other words, the claim implies that organisms are able to adapt instantaneously to novel conditions. This is in contradiction to the basic principles of evolution, namely, that natural selection acts on variation in a population, resulting in well-adapted traits *over the course of generations* (e.g., Cosmides and Tooby 1995; Dewsbury 1992, p. 98; Symons 1992; Tooby and Cosmides 1990b). For example, the presence of large predatory fish forms a selection pressure for small fish to become larger. This does not mean that little Nemo actually grows bigger. It means that if little Nemo is slightly larger than his friends are, he has a higher chance of surviving and propagating his genes than do smaller fish. Given that size is linked to genes, the following generation will contain a larger proportion of slightly bigger fish. As long as the selection pressure of large predatory fish is present, and as long as there are no conflicting selection pressures, new generations of fish will have a larger average size than the previous ones. In retrospect, this process can be summarized as small fish maximizing their fitness by becoming larger. They are not actually maximizing fitness, however; they are only expressing the body plan that was selected in previous generations. The same argument holds for human behavior: *humans are adaptation-executioners, not fitness-strivers* (Tooby and Cosmides 1990b, p. 420; see also Barkow 1990, p. 344).

The assumption that individuals are fitness maximizers is also present in such phrases as, "animals have an ability to learn how to maximize fitness," "their flexibility allows them to learn the best response," "humans have a capacity for culture," and "human consciousness enables us to maximize fitness" (Cosmides and Tooby 1995). All of these statements are black-box explanations, as they do not explicate *how* organisms maximize fitness. Upon explication of the mechanism,

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[2] The concept of individuals as fitness maximizers is adopted from the behavioral ecology tradition in biology, which rarely addresses the difference between the ancestral and the current environment. One possible explanation for this difference in focus is that the concept of the EEA is more relevant to human adaptations, as cultural and technological changes have outpaced organic evolution more in humans than in any other species (e.g., Tooby and Cosmides 1989, p. 35; Symons 1990). Others have argued, however, that behavioral ecologists would also benefit from focusing more on ancestral conditions, as there are also mismatches between the contemporary environments and the EEAs of non-human animals (e.g., Crawford 1993; Daly and Wilson 1999).

these explanations become problematic. The following paragraphs discuss two additional explications of such mechanisms: learning and consciousness.

The view that animals are like blank slates, acquiring information about how to maximize fitness through a process of trial-and-error learning is problematic because such a process would be extremely inefficient (Cosmides and Tooby 1995). For example, what should you do when you are confronted for the first time in your life with a large fanged animal approaching? Talk to it? Stand on your head? It seems highly unlikely that, from an almost endless number of responses, you would randomly pick one that would promote your survival and allow you to bring your newly learned response into practice in a subsequent encounter. A less ridiculous account may point to the ability to imitate or learn adaptive behavior from parents or co-specifics. However, imitation or learning only leads to adaptive behavior if the teachers have already solved the adaptive problem. This does not mean that evolutionary psychology denies the power of learning. It only denies that our learning is domain-general – that our minds are completely blank and absorb any information that is presented to them. Section 4.2.1 discusses the evolutionary psychological view of learning in more detail.

Human consciousness is a second mechanism that has been proposed as a general fitness maximizing system. According to this argument, human consciousness enables us to plan, to formulate goals, and to oversee the consequences of various courses of action (scenario-building), thereby helping us to adapt quickly to novel conditions (e.g., Alexander 1990; Turke 1990). Again, evolutionary psychologists do not deny that consciousness and its associated qualities are important adaptations. However, the ability to plan, to formulate goals, and to build scenarios does not imply the pursuit of fitness maximization. According to evolutionary psychologists, we do not pursue the general goal of fitness maximization, but rather a large number of intermediate goals that have evolved in the process of natural selection, including the desire for sex, the need to belong, and the tendency to care for our offspring (Symons 1992).

2.3 The importance of emotions

The previous section elaborated on the arguments that evolutionary psychologists provide for the concept of domain-specific psychological mechanisms. This section focuses on describing these mechanisms. As mentioned above, emotions play an important role in these mechanisms.

The function of emotions has received considerable attention within the field of social psychology. According to Plutchik (1962, p. 151), an emotion is "a

patterned bodily reaction of either destruction, reproduction, incorporation, orientation, protection, reintegration, rejection or exploration or some combination of these, which is brought about by a stimulus. Emotions are typically transient, adaptive, biological reactions which are usually (but not necessarily) triggered by external stimuli." Lazarus (1991, p. 38) defines an emotion as a complex disturbance that includes three main components: subjective affect, physiological changes related to species-specific forms of mobilization for adapted action, and action impulses having both instrumental and expressive qualities. According to Frijda (1986, p. 371-372), emotions are changes in action readiness in response to events that are relevant to the individual's concerns. These concerns are, to some extent, a reflection of his or her biological interests. Finally, Cosmides and Tooby (2000, p. 93) define an emotion as a super-ordinate program whose function is to direct the activities and interactions of the subprograms governing perception, attention, inference, learning, memory, goal choice, motivational priorities, categorization and conceptual frameworks, physiological reactions, behavioral decision rules, and many other processes (see also Nesse 1990; Parker 1998; Scherer 1996).

All these definitions agree on at least three points. First, emotions have a bodily component. Second, they form the link between cues and responses. Third, emotions are the result of selection processes; they have evolved to cope with specific fitness-relevant situations. Note that a definition including these elements points does not exclude non-human animals from having emotions. Plutchik (2003, p. 225-226) thus states, "[a]ll organisms have sensors that detect special chemicals as well as gradients of intensity. All organisms have start and stop mechanisms that determine the beginning and end of actions. […] Given the fact that emotions are forms of adaptation made to environmental events, is there any reason to limit the application of the term to humans?" (see also Cosmides and Tooby 2000).

Many scholars have described the relevant cues and adaptive consequences of specific emotions. For example, love is triggered by the long-standing and stable presence of another person (particularly a mate), urging us to stay with this person even in the presence of attractive alternatives (Frank 1988; Nesse 1990). Guilt is triggered by the ill treatment of another person by the subject, and functions to urge reparation of the relationship (Eisenberg 2000; Fessler and Haley 2003; Lewis 1993; Parker 1998). Shame is a stronger form of guilt and leads individuals to avoid those whom they have harmed (Eisenberg 2000; Lewis 1993). Finally, anger is triggered by harm done by another person, and leads to behavior aimed at punishing the offending person (Nesse 1990; Trivers 1971).

But do we really need emotions? Couldn't we survive with specific programs linking each cue to the adaptive response without the intervention of an emotion? In other words: It's fine that my body tells me to withdraw my foot if I step on a thorn, but why does it have to hurt so much? Why don't we simply have a program that leads us to withdraw our foot if it makes contact with an object that damages the upper skin layer? These questions actually touch on two different issues, and answering them requires that we distinguish between emotions and feelings. An emotion is the internal program that links cues with responses. A feeling is the subjective experience that accompanies an emotion (Cosmides and Tooby 2000; Damasio 1994, 2000).

The answer to the question, "Do we need emotions?" is therefore an unequivocal "yes." We need emotions for the same reason that we need domain-specific mechanisms. Without them, there would be no mechanism for linking fitness-relevant cues to responses. We would somehow need to know, or learn through trial and error, the responses that would be most suitable in each situation. Damasio (1994) made a similar argument, asserting that it is simply impossible to select the appropriate response from all possible responses. Emotions function to highlight the one that has proved to be the best response in the past.[3] A number of case studies of people with neurological impairments provide evidence that the absence of emotions is associated with an inability to make decisions (Damasio 1994).

The question, "Why do we suffer if we step on a thorn?" boils down to the question, "Why do we have feelings?" Its answer is less straightforward. Given that feelings are not prerequisites for emotions, they may seem unnecessary and even burdensome in some cases. According to Damasio (2000, p. 284-285), however, this is incorrect. Feelings are incentives to heed the consequences of an emotion – in the case of pain, to tend the wound and protect it while it is healing. In his view, the emergence of consciousness served to extend the reach of an emotion even further. *Knowing* that we have feelings associated with an emotion forms a much stronger incentive than would the *feeling* of an emotion alone. This allows us to plan specific and non-stereotyped responses that can either

[3] The phrase "in the past" is left ambiguous on purpose. In his book, *Descartes' error*, Damasio argued that at least our secondary or social emotions are the result of learning processes in the past (Damasio 1994, p. 174), suggesting some form of the trial-and-error learning that I just criticized. In his later work, *The feeling of what happens* he corrected this confusing claim by emphasizing that secondary emotions are not solely the result of education within a culture. They are biologically preset, either partly or mostly. Because many emotions appear only later in human development (e.g., guilt or shame), however, environmental factors appear to play an important role (Damasio 2000, note 13 of chapter 2). Anticipating the argument on the interactions between nature and learning (see Section 4.2.1), we might say that humans are *biologically prepared* to learn to feel guilt and shame.

complement the emotion or guarantee that the immediate gains brought by the emotions are maintained over time.

3 Reciprocal altruism

The subject of altruism has been of major importance in sociobiology and evolutionary psychology. The founding father of sociobiology, Edward O. Wilson, described it as the central theoretical problem of sociobiology: "How can altruism, which by definition reduces personal fitness, possibly evolve by natural selection?" (Wilson 1975, p. 3). Part of the answer to this question lies in the theory of kin selection (Hamilton 1964), in which the adaptiveness of altruistic behavior is presented as a linear function of the genetic relatedness to the beneficiary. To explain altruism between unrelated individuals, Robert Trivers (1971) introduced the term *reciprocal altruism*. Trivers argued that providing a benefit to a non-related individual is beneficial to an actor's fitness if the costs of this action are lower than the benefits received in return over the long term. Individuals who are willing to provide benefits to non-related others are better off in the long term than are individuals who reap benefits from altruistic others without bothering to reciprocate, *provided that altruists respond to cheaters by curtailing all future possible altruistic gestures to such individuals* (Trivers 1971, p. 36).

When Trivers formulated his theory, evolutionary psychology did not yet exist. Although he presented a psychological system underlying reciprocity, and although he noted that a hominid species in the Pleistocene period would have met the preconditions for the evolution of reciprocal altruism (for example, life in small, mutually dependent social groups), his focus was on the benefits and (especially) the potential costs of reciprocal altruism in the present environment. Also most later scholars deduced the specific mechanism or strategy of reciprocal altruism by using a game theoretical argument, rather than by analyzing specific adaptive problems in the ancestral environment. The next section provides a discussion of this conventional mechanism of reciprocal altruism, including a review of the empirical support. Section 3.2 discusses a number of criticisms of the scorekeeping account. Section 3.3 introduces an alternative mechanism that incorporates ancestral selection pressures. The discussion concludes with Section 3.4, which addresses the question of how these two mechanisms are related.

3.1 The scorekeeping mechanism

The basic argument underlying the scorekeeping mechanism is that a group of mutually sharing individuals is vulnerable to free-riders. In a group of generous individuals, a free-rider, who gladly accepts the benefits of his generous group members without returning anything, is better off in terms of time and resources. Consequently, she has higher reproductive fitness. The only way to avoid exploitation by free-riders is to use a *conditionally cooperative* strategy: to make cooperative behavior *contingent* on the behavior of the other. Thus, if someone shares food with me, I will then share with that person as well. If the other does not return a benefit when I have shared with her, she is apparently a free-rider and should be excluded from sharing (Cosmides and Tooby 1992; Reeve 1998; Trivers 1971).

According to the scorekeeping account, one's behavioral response in such a situation is based on (unconscious) calculations regarding the amount of benefits one has provided to another individual and the amount of benefits received from this person. In the case of an unfavorable imbalance, (i.e., if the benefits one has provided exceed the benefits one has received) any further benefits are suspended until the other has restored balance.

Individuals also attempt to restore balance in the opposite situation. A favorable imbalance, therefore, compels an individual to restore balance by *providing* benefits to the other person (Boehm 1999, p. 183-184; Bugental 2000, p. 199-200; Krebs 1998, p. 347). The reason being that if a person acts only on unfavorable imbalances, while ignoring (or even pursuing) favorable imbalances, his interaction partners will conclude that the person is a free-rider and refuse to provide any more benefits.

Although the scorekeeping mechanism presumes some cognitive abilities, it does not necessarily rely on purely calculative processes. Unfavorable imbalances may elicit emotions of indignation or even anger. These emotions, in turn, trigger behavioral responses aimed at restoring balance (Nesse 1991; Parker 1998). On the other hand, favorable imbalances may lead to compensating behavior through emotions of gratitude and obligation or, in the case of longer standing debts, shame, guilt, and humiliation (Nesse 1991; Parker 1998; Pinker 1998; Trivers 1971).

The scorekeeping mechanism is strongly rooted in game theory. When Trivers introduced the concept of reciprocal altruism, he referred to the analogy with the Prisoner's Dilemma, as introduced by Luce and Raiffa (1957), and Rapoport and Chammah (1965) (for an elaboration of the Prisoner's Dilemma, see Chapter 2, note 2; and Chapter 3). Trivers' concept of reciprocal altruism was

identical to the optimal strategy in an iterated Prisoner's Dilemma (Trivers 1971, p. 38). More recently, evolutionary game theorists confirmed the success of a reciprocal altruistic strategy. In a study by Axelrod (1984), simulated actors with different strategies competed in iterated Prisoner's Dilemmas. The most successful strategy was a strategy called "Tit-for-Tat," which cooperated on the first move and thereafter imitated the move of its interaction partner. Thus, it rewarded cooperative behavior with cooperation and punished defecting behavior with defection. This strategy came to be known as the embodiment of Trivers' reciprocal altruism.

Following Axelrod's tournaments, many mathematical and simulation studies have been conducted with other payoff matrices, additional parameters, large groups instead of dyads, different strategies, et cetera (e.g., Boyd and Richerson 1988; 1989; Hayashi 1993; Kollock 1993; Nowak and Sigmund 1993; Roberts and Sherrat 1998; for a critical review, see Gotts et al. 2003). In general, these studies agree that, by the nature of the game, cooperative actors are able to withstand non-cooperative actors only if they make their behavior *conditional* on the behavior of their interaction partners (i.e., by adopting some form of Tit-for-Tat-strategy or by keeping track of each other's contributions) (Brown 1983; Dugatkin 1997).

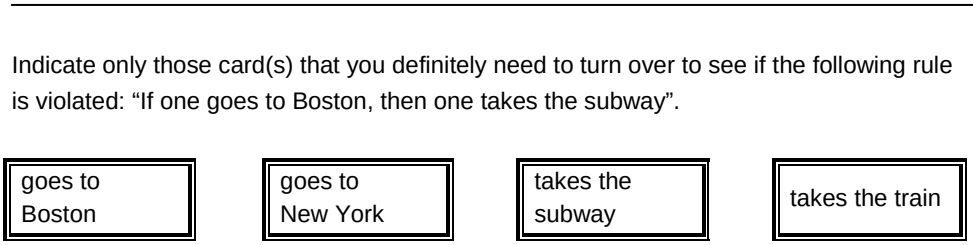
Studies from several fields show that people actually behave according to such a scorekeeping mechanism. Exchange experiments have shown that subjects do indeed match the benefits they provide to the benefits provided by their interaction partners (Chertkoff and Esser 1976; Galluci and Perugini 2000; Komorita and Esser 1975; Pruitt 1968; Rapoport and Chammah 1964). Support for the avoidance of advantageous imbalances, or *overbenefiting*, is provided by studies in the field of equity theory (Griffeth et al. 1989; Walster et al. 1973; Walster et al. 1978). Many studies have shown that people avoid asking others for help if they are unable to repay them (Castro 1974; Greenberg and Shapiro 1971; Morris and Rosen 1973), are more motivated to offer help to a person if this person has helped before (Greenberg and Bar-Tal 1976; Gross and Latané 1974; Shumaker and Jackson 1979), and experience negative emotions after overbenefiting (Bar-Tal and Greenberg 1974; Buunk et al. 1993; Castro 1974; Gross and Latané 1974; Shumaker and Jackson 1979).

The only study that makes an explicit attempt to demonstrate that humans have a domain-specific psychological mechanism for scorekeeping is Cosmides and Tooby's cheater detection study (Cosmides 1989; Cosmides and Tooby 1992). Cosmides and Tooby argued that, if humans have evolved a domain-specific psychological mechanism to cope with the presence of cheaters, they should be

extremely sensitive to situations in which there is a possibility of being cheated. Following experiments by Peter Wason (1966), they presented subjects with a conditional "if … then" rule concerning either a descriptive rule (e.g., "If one goes to Boston, then one takes the subway"), or a rule involving a social contract (e.g., "If you take the benefit, then you pay the cost"). They then asked which of four cards should be turned over to determine if the rule was violated. For example, the correct logical solution for the "If one goes to Boston, then one takes the subway" rule is to turn over the "goes to Boston" (P) and "take the train" (not Q) cards (see Figure 1.1).

The results of their experiments showed that persons are much better at detecting violations of rules that have the form of a social contract than they were at detecting violations of descriptive rules. Cosmides and Tooby (1992) interpreted this as support for the hypothesis that humans have a domain-specific mechanism for detecting cheaters (see also Gigerenzer and Hug 1992).

Figure 1.1: Example of the Wason selection task



The idea that reciprocal altruism takes the form of scorekeeping has also pervaded into other disciplines. Since the sharing of food is often mentioned as the prototypical instance of scorekeeping behavior, anthropologists have used field data to test this idea (see for a review Gurven 2004). Primatologists have also been interested in demonstrating scorekeeping behavior in their research subjects (for a review, see Brosnan and de Waal 2002). Given that human and non-human primates are closely related, evidence of scorekeeping among non-human primates would imply that the evolutionary origins of this behavior are very old. Section 3.2.2 discusses the problem of assessing contingency that is present in many of these anthropological and primatological studies. Chapter 2 elaborates further on anthropological studies concerning scorekeeping reciprocity and the validity of their conclusions.

3.2 Criticisms of the scorekeeping account

The idea that reciprocal altruism is governed by a scorekeeping mechanism has been influential in evolutionary psychology. Analyses of cooperation between unrelated individuals usually consider the interaction partners to be scorekeepers or cheater detectors. A number of criticisms can be made on this account, however. The following sections argue that not all relations are governed by scorekeeping considerations, that the empirical evidence for the scorekeeping mechanism is not as strong as has been suggested, and that the scorekeeping explanation ignores ancestral selection pressures.

3.2.1 Friends do not keep scores

Recently, several authors have begun to question the ubiquity of scorekeeping. An important example of a relationship involving the mutual provision of benefits concerns the relationship between friends. However, a defining feature of friendships is that they are *not* characterized by scorekeeping. According to Tooby and Cosmides (1996), scorekeeping behavior is restricted to the *exchange domain*, which is characterized by explicit contingent exchange and turn-taking reciprocation. Altruistic adaptations in the *friendship domain* do not map unto the structure of tit for tat or any other standard model of reciprocal altruism. Instead, friendships are characterized by a spontaneous pleasure in helping the other, without looking for a contingent return (Tooby and Cosmides 1996, p. 131, 139). Silk (2003, p. 37) makes a similar point, stating, "Tit-for-Tat reciprocity is antithetical to the formation and maintenance of close friendship."

These remarks are consistent with the prevalent social science definition of friendship, which emphasizes non-instrumentality and concern for the other. For example, Hays (1988, p. 393) puts forth the following argument: "[t]he primary goal of the interdependence between friends is social-emotional rather than instrumental, meaning that friends derive satisfaction from their interactions themselves (e.g., in the form of companionship, stimulation, belongingness, emotional support), rather than engaging in interactions primarily to achieve an ulterior motive." Similarly, Allan (1979, p. 43) observes that "individuals can be useful because they are friends, but not friends because they are useful." A study by Hays (1985) suggests that friends even value the costs that are associated with this relationship. Friendship intensity appeared to be more highly correlated with benefits-plus-costs-scores than with benefits-minus-costs-scores. In addition, a

strong concern for maintaining a balanced relationship may be considered a betrayal of the friendship (Shackelford and Buss 1996)

The distinction between an exchange domain and a friendship domain, as present in the reasoning by Tooby and Cosmides (1996) and Silk (2003), is similar to a common distinction in the social science literature. Clark and Mills (1979; see also Clark and Grote 2003) distinguish between *exchange relationships* and *communal relationships*. Communal relationships, which typically involve relationships with family members, romantic partners, and friends, are characterized by mutual concern for the welfare of the other person and a positive attitude toward helping the other in times of need. Exchange relationships, on the other hand, which typically exist between acquaintances, strangers, and business partners, are characterized by the obligation to reciprocate a benefit received with a comparable return benefit (for similar distinctions, see Bugenthal 2000; Deutsch 1975; Ekeh 1974; Fiske 1992; Lindenberg 2000; Sahlins 1972; Weiss 1998). Support for this distinction comes from studies in the fields of equity theory and distributive justice theory, which show that friends are less interested in maintaining balanced relationships than are strangers or individuals who are more distant (Clark 1984; Greenberg 1983; Lerner 1974; Morgan and Sawyer 1979; Roberto and Scott 1986a). Further, they are more concerned with responding to each other's needs (Clark et al. 1989; Lamm and Schwinger 1980, 1983).

In contrast to these studies, another tradition explicitly extends the assumptions of equity theory to the realm of close relationships. Based on the notion that inequitable relationships lead to distress (Walster et al. 1973), this tradition predicts that individuals who perceive their relationship as equitable are more satisfied with the relationship and experience less loneliness than do individuals who feel overbenefited or underbenefited (for a review, see Buunk and Schaufeli 1999). Many studies have found support for this hypothesis, in both intimate relationships (Hatfield et al. 1985; Sprecher 1992; van Yperen and Buunk 1990) and friendships (Buunk and Prins 1999; Roberto and Scott 1986b; Rook 1987a). Although these studies apparently contradict the claim that people involved in close relationships do not keep scores, it is important to note that such studies mainly consider socio-emotional benefits, as opposed to such instrumental benefits as physical effort or material resources. For example, Walster, Walster, and Traupmann (1978; see also Hatfield et al. 1979) introduced a "global measure" which simply asks subjects to indicate what kind of "deal" they are getting in their relationship, considering their inputs and outputs and their partner's inputs and outputs. When answering this question, individuals tend to focus on socio-emotional contributions, including companionship, liking and loving, acceptance,

commitment, and attentiveness (Smith and Schroeder 1984; van Yperen and Buunk 1990). These benefits are quite different from the instrumental benefits that are typically associated with scorekeeping and cheater detection. Whereas instumental benefits concern instances of somatic effort, which have (or had) a direct effect on an individual's fitness, socio-emotional benefits coincide with the proximate goals or emotions that individuals pursue. As a consequence, such benefits are highly confounded with the notion of a bonding mechanism, as described in Section 3.3.

In summary, there are strong indications that scorekeeping does not occur in all relationships that involve the exchange of benefits. Reciprocal altruistic interactions between friends are apparently governed by a psychological mechanism other than scorekeeping: a bonding mechanism (see Section 3.3).

3.2.2 Absence of strong support for scorekeeping

Although considerable evidence exists to support the presence of a scorekeeping mechanism (see Section 3.1), a closer look at some of those studies casts doubts on their conclusions. The following sections discuss the validity of the anthropological and primatological studies on reciprocal altruism and scrutinize the cheater detection study of Cosmides and Tooby.

Problems with assessing contingency

The scorekeeping mechanism concerns the *contingent* exchange of benefits. Many studies that report evidence of scorekeeping behavior, however, do not actually assess contingency. The majority of anthropological and primatological studies are restricted to analyses of correlations between benefits provided and benefits received. This is problematic, as a positive correlation between benefits provided and benefits received does not necessarily indicate contingency. It could also be the result of a mutual preference for providing benefits to close associates, or *friends*. To disentangle these explanations, de Waal and Luttrell (1988) made a distinction between *calculated* and *symmetry-based reciprocity*, which is very similar to the distinction between scorekeeping and bonding mechanisms. Calculated reciprocity is regulated by feedback; the continuation of helpful behavior is contingent upon the partner's reciprocation. In contrast, symmetry-based reciprocity involves exchanges between closely bonded individuals who help each other without stipulating equivalent returns (p. 103).

Other studies present partial correlations, or regression coefficients, thereby controlling for such variables as time spent in association (e.g., de Waal

and Luttrell 1988) or residential distance (Gurven 2000b). However, to really distinguish between symmetry-based and calculated reciprocity, one should either study time-sequenced instances of providing benefits, or experimentally create an imbalance between benefits provided and benefits received, and subsequently determine whether the subjects attempt to restore a balance (e.g., de Waal 2000).

As argued in Chapter 2, keeping this restriction in mind, we see that most anthropological studies fail to demonstrate scorekeeping behavior. The primatology literature, in contrast, includes a number of time-sequenced studies (de Waal 1997a, 1997b, 2000), as well as one study involving an experimental manipulation of the balance between benefits provided and benefits received (Hemelrijk 1994).

In the latter study, grooming behavior of long-tail macaques was manipulated by smearing them with a sticky substance, and then provoking aggressive interactions. It was found that, if A had been groomed by B, he was more likely to provide support to B than he was if he had not been groomed. However, since Hemelrijk's study did not address the question of whether A's willingness to intervene in a conflict was *restricted* to B, a good-mood explanation may also account for this result. This explanation argues that the receipt of benefits leads to an indiscriminate increase in beneficial behavior (de Waal 1997a, p. 384).

In a study among chimpanzees, de Waal (1997b) found that subjects who had been groomed in the past hour were more likely to share a bundle of branches and leaves (provided by the experimenter) with their previous groomers. Since subjects restricted their sharing to their previous groomers, the good-mood explanation does not hold. An explanation in terms of symmetry-based reciprocity still cannot be excluded, however. If we assume that subjects have a small number of close associates, this might result in both preferential grooming and preferential sharing with those associates, without sharing being the *consequence* of being groomed.

Another study by de Waal (2000; see also de Waal 1997a) challenges this alternative explanation. De Waal conducted sharing experiments with pairs of capuchin monkeys, one of whom had access to a bowl of food. Roles were reversed several times, such that each monkey had access to food a number of times while the other had not. Correlations between sharing rates between the different test phases were positive. Because the effect of pre-existing affiliative tendencies between the two individuals was held constant, this study provides some support for the existence of a crude mechanism of calculated reciprocity.

In a related vein, Chapter 4 investigates whether helping behavior among human subjects can best be described as symmetry-based reciprocity (bonding) or

by calculated reciprocity (scorekeeping). The results of two scenario experiments are reported, in which subjects were asked to imagine a situation in which they are indebted to another person, or in which another person is indebted to them. The situation and the answering categories were constructed in such a way that one's response indicated either a bonding or a scorekeeping response.

Criticism on the cheater detection mechanism

Cosmides and Tooby's famous study on cheater detection has been severely criticized on logical grounds (Davies et al. 1995; Holcomb 1998; Stenning and van Lambalgen 2004; van Lambalgen 2004). Although these criticisms are important, as they question the presence of a domain-specific psychological mechanism for cheater detection, most evolutionary psychologists seem to be unaware of them.

As discussed in Section 2.1, Cosmides and Tooby (1992) argue that, if individuals have a domain-general mechanism for logical reasoning, they should perform equally well on two conjectures of the same logical form, regardless of content. Because people perform much better on social contract rules (e.g., "If you take the benefit, than you pay the cost") than they do on descriptive rules (e.g., "If one goes to Boston, than one takes the subway"), Cosmides and Tooby conclude that humans have no domain-general mechanism for logical reasoning. Instead, they have a domain-specific mechanism for detecting violations of social contracts. Although Cosmides and Tooby claim that the descriptive rule has the same logical form as the social contract rule, they differ in some crucial aspects. These differences, and not the fact that our minds are equipped with a cheater detection mechanism, might be responsible for the difference in performance. For example, the two rules differ in that one is descriptive and the other is prescriptive. Whereas a descriptive rule describes a state of the world that is either true or false, a prescriptive rule has no truth value. As a consequence, a descriptive rule needs only one violation to be falsified. For prescriptive rules, the violation of the rule by one card is independent of whether another card violates the rule. This difference might have had the result that subjects in the descriptive rule condition were satisfied after picking one card, while subjects in the social contract rule condition did not stop after detecting one violation, but also considered the remaining cards (Stenning and van Lambalgen 2004; van Lambalgen 2004). In a replication of Cosmides and Tooby's experiments that eliminated this and other sources of confusion, Stenning and van Lambalgen (2004) found a strong increase in the performance on the descriptive rule.

Even more important, according to Stenning and van Lambalgen (2004; see also van Lambalgen 2004), is that Cosmides and Tooby endorse an incorrect conception of logic. They assume that, if humans have a domain-specific mechanism for logical reasoning, it takes the form of classical propositional logic, including the accompanying semantics and truth tables that define the validity of arguments. Classical propositional logic is only one of many possible logical systems, however. Before applying logic, a person first has to determine the appropriate logical form, which is obviously not trivial in the Wason selection task. Stenning and van Lambalgen (2004, p. 483) therefore conclude that "Wason got his own task wrong in stipulating that there was a particular 'obviously correct' answer." In summary, it is possible to reason logically without using classical propositional logic. This implies that the correct use of classical propositional logic is not a precondition for a domain-general mechanism for logical reasoning.

3.2.3 The scorekeeping mechanism ignores the ancestral environment

As mentioned before, the scorekeeping mechanism is based on the argument that, although each person is better off in situations in which everybody helps each other than they are in situations in which nobody helps anyone, each person benefits even more by reaping the benevolence of others without paying the costs of repaying their help. As a consequence, helpful individuals can only withstand the constant threat of exploitation if they keep account of benefits provided and benefits received with regard to each individual.

This argument, however, is based on an overestimation of both the expected benefits of cheating and the expected benefits of scorekeeping. These estimations are based on a Prisoner's Dilemma situation – an environment in which unrelated actors are assigned to interaction partners and are forced to make a decision either to cooperate or to defect (or, as in delayed games, they take turns making moves). If we take the living conditions in the ancestral environment into account, it becomes clear that both the expected benefits of cheating and the expected benefits of scorekeeping are lower than is generally suggested (see Section 2.1.2).

Our ancestors lived in small, kin-based groups in harsh conditions. Predators lurked and food was *patchily distributed*: finding food was difficult, but when it was found, there was usually more than one individual could consume. Under these conditions, *the expected benefits of cheating would have been small*. First, the costs of sharing food were relatively low (Tooby and Cosmides 1996). Although finding and killing an animal was difficult, each captured animal yielded enough

meat for several individuals. Moreover, the meat could not be stored, so the finder of the food gained nothing by refusing to share. Second, since groups were based on kinship, cheating the members of one's group would often amount to cheating one's own kin. Third, considering the harshness of conditions, groups containing a large number of cheaters were at considerable risk of extinction. In general, such group selection arguments are considered invalid, as the individual benefits that a cheater may accrue override the effects of between-group selection. Under some conditions, however, the effects of between-group selection have been shown to be stronger than the effects of within-group selection (Sober and Wilson 1998; Wilson and Sober 1994). If groups are demographically closed or have low phenotypic variation (e.g., because individuals tend to imitate or conform to the behavior of the majority), and if competition between groups is high or groups run a high risk of extinction, groups of generally cooperative individuals surpass groups containing mainly cheaters. It is plausible that these conditions applied to the hominid groups in the ancestral environment (Boehm 1999; Fehr and Fischbacher 2003; Gintis 2000; Gintis et al. 2003; Richerson and Boyd 1998).

Consideration of ancestral conditions also leads to an adjusted notion of the *expected benefits of scorekeeping*. Scorekeeping is a useful strategy in situations in which interaction partners call upon each other in predictable, systematic ways. The exemplary model of such a situation is the delayed Prisoner's Dilemma, in which two actors take turns deciding whether to cooperate or defect. In contrast, the Pleistocene savanna was anything but predictable. Due to the patchy distribution of food, the risk of failing to find any food on a number of subsequent days was considerable. An individual who kept track of the benefits that she and her interaction partner provided and who avoided giving benefits if the other still owed her would run the risk of losing a committed interaction partner. This could result either from driving the other to seek interaction partners who were less concerned about balanced exchange or – even worse – by letting the other perish when there was nowhere else to turn. In the words of Tooby and Cosmides, "[T]he ability to attract assistance during such threatening reversals in welfare, where the absence of help might be deadly, may have had far more significant selective consequences than the ability to cultivate social exchange relationships that promote marginal increases in returns during times when one is healthy, safe, and well-fed" (Tooby and Cosmides 1996, p.132).

The last argument is investigated in Chapter 3, which reports the results of a series of simulations. In these simulations, a strict scorekeeping strategy is imposed on an environment in which actors experience the need for help in an unsystematic and unpredictable way, and where they must select their helping

partners rather than having them externally assigned. The results of these simulations are compared to those of simulations that feature a strategy that is less concerned with keeping scores and more concerned with sticking to actors who have proved to be most helpful in the past, with regard to both providing and asking for help.

3.3 The bonding mechanism

Whereas the scorekeeping mechanism proceeds from an analysis of costs and benefits associated with different strategies in a game theoretical environment, the bonding account is more closely attuned to the living conditions of our ancestors. For this reason, it is more firmly based on evolutionary psychological arguments than is the scorekeeping account.

The central idea underlying the concept of a bonding mechanism is that the Pleistocene savanna exerted selection pressures for social group living. Food resources were patchily distributed, making an individual's foraging success unpredictable, and isolated individuals were more vulnerable to predator attacks than were those who lived in groups. As a consequence, individuals equipped with mechanisms that supported the maintenance of group membership were therefore more likely to survive and reproduce than were those without such mechanisms (cf. Baumeister and Leary 1995; Caporael et al. 1989; Smith et al. 1999; Smith, Coats, and Murphy 2001). Moreover, the high level of interdependence forced individuals not only to reap the benefits of group membership, but also to care for the survival and well-being of their group members. As argued above, ignoring a group member's need for help could result in the loss of a valuable protective and reciprocity partner (Tooby and Cosmides 1996).

Therefore, the bonding mechanism generated not only feelings of attachment toward one's group members, leading an individual to stay with the group, thereby *receiving* the benefits of protection and food sharing. It also generated feelings of commitment and care, resulting in the *provision* of benefits to group members. It is plausible that the bonding mechanism was originally based on pre-existing adaptations for care toward kin and attachment toward caretakers (Bowlby 1969), and evolved to extend such emotions and behaviors toward sexual partners and unrelated but familiar others as well (Panksepp 1998; Zeifman and Hazan 1997).

The central cues for a bonding mechanism include both the *needs* of the other person and the *relationship with the other*. When confronted with a group member who was in need of help, individuals would respond with helping

behavior, even if such help would result in an imbalanced relationship. This does not imply, however, that the relationships would not be balanced over the long term. On the contrary, because even the best hunter had a fair chance of failing in capturing game, responding to each other's needs would have produced a situation in which the frequency with which each group member helped others would be approximately equal. The difference with the scorekeeping mechanism is that helping behavior depends on the needs of the other person rather than on the difference between benefits provided and benefits received.

In the ancestral environment, individuals spent most of their lives in the same group. It is plausible therefore, that *every group member* triggered the emotions of commitment and care, and the appropriate bonding behavior, when in need. In the present environment, group membership is no longer so clear. The most appropriate translation of "an individual's group" would be the circle of that individual's closest affiliates (i.e., friends and family). When one of those persons is in need, emotions of commitment and care will be triggered, resulting in a willingness to provide help, regardless of possible imbalances.

3.4 How do the scorekeeping and bonding mechanisms relate to each other?

The presentation of scorekeeping and bonding as two alternative mechanisms of reciprocal altruism raises the question of how the two mechanisms might be related. Are they two mechanisms that co-exist on the same level, both originating in the evolutionary past, or does one predominate in terms of evolutionary origins? The first possibility is implicit in many accounts that interpret behaviors or considerations that are equivalent to scorekeeping and bonding as two algorithms that have evolved to cope with specific problems (e.g., Bugenthal 2000; Ten Houten 1999), or two norms that are associated with different domains of life (e.g., Clark and Mills 1979; Deutsch 1975; Fiske 1992), or two goal-frames that can vary in salience according to the context of the situation (Lindenberg 1990, p. 743; 1993, p. 29; 1999; but see Lindenberg 2001, p. 661, for a priori differences in the salience of frames). Considering the accounts of both mechanisms provided in the previous sections, it is unlikely that scorekeeping and bonding are two complementary mechanisms with equal evolutionary primacy. The bonding mechanism was explicitly introduced as an alternative to the scorekeeping mechanism, which was criticized for ignoring the ancestral environment.

However, if we assume that the ancestral environment gave rise to a psychological mechanism for bonding behavior rather than to a psychological

mechanism for scorekeeping behavior, how are we to explain the numerous instances of scorekeeping that we encounter every day? A speculative answer to this question is that scorekeeping behavior is a cultural adaptation to the demands of market society. The emergence of sedentary societies, about 10,000 years ago, marks the start of the development of market society. Characteristic of this shift from a nomadic existence to a sedentary way of life was that the acquisition of food through hunting and gathering practices was more and more replaced by people producing their food themselves. This went hand in hand with domestication of plants and animals, and as a consequence, with storage of food and property rights of land and livestock . These conditions set the stage for the emergence and expansion of market society (cf. de Vos and Wielers 2003; Diamond 1999).[4]

According to de Vos and Wielers (2003; see also de Vos 2004), while humans are able to act according to economic reason, doing so takes effort, and it is therefore easy to fall back into older modes of behavior (e.g., bonding behavior). A similar argument is provided by Elizabeth Hoyt, a forgotten economist who used insights from psychology, economics, and cultural anthropology to demonstrate that, in spite of influential accounts of humans as economic exchangers by nature (Malinowski 1926; see also Ofek 2001), economic rationality is not basic to human nature, but must largely be learned instead (Hoyt 1926). The first exchanges among humans involved gifts and intimate personal services provided out of good will, and were based on the ability of the giver and the need of the receiver. From this, Hoyt concludes that "[t]he transformation of the standard of valuation from good will to utility was a matter of learning and was brought about through the extension of trading relations" (p. 95).

De Vos and Wielers (2003) provide two arguments in favor of the evolutionary primacy of bonding behavior. First, the resistance to market expansion that existed (and still exists) - including the historical suspicion toward traders and attempts to construct communities shielding against market intrusion - may be interpreted as an indication of the large amount effort it takes to learn behaviors that are novel in an evolutionary sense. Tooby and Cosmides (1996, p. 139) make a similar point, arguing that "[t]he widespread alienation many feel with modern society is the result of an evolved psychological mechanism that experiences this level of explicit contingent exchange in our lives as a message about how deeply (or rather, how shallowly) we are engaged with others."

[4] Note that this notion of market society is different from the conception that market society is a phenomenon of the last centuries. The emergence of market society should be seen as strectching much further back in time than the Industrial Revolution or the Renaissance, or even antique Greece.

Second, they refer to exchange experiments that demonstrate the tendency of individuals to attach higher priority to bonds with their interaction partners than to monetary benefits. Kollock (1994) found that subjects preferred offers from interaction partners with whom they had interacted for a number of rounds to better offers from new interaction partners, even under conditions in which the risk associated with changing partners was low. Similarly, Lawler and Yoon (1996; 1998; see also Lawler et al. 2000) found support for the hypothesis that frequent exchanges lead to positive emotions, the perception of the relationship as a valuable object on its own, and to behaviors that express commitment (e.g., staying with the interaction partner in spite of better offers, contributing to joint ventures, and giving gifts).

The study reported in Chapter 4 includes an attempt to test the hypothesis that bonding is an evolved psychological mechanism, while scorekeeping is not.

4 Evolutionary psychology and sociology

Few sociologists have incorporated ideas from evolutionary psychology into their theories (e.g., Lord and Sanderson 1999; Sanderson and Ellis 1991). Given that sociology is the study of human society and social phenomena, this seems somewhat surprising. Many critics of sociology have addressed the possible causes of this reluctance, focusing on the historical development of sociology (e.g., Ellis 1996; Lopreato and Crippen 1999, p. 52; Pearson 1996; Sanderson 2001, p. 137; Urdry 1995; Wielers and de Vos 2003), or on ideological issues (e.g., Carey and Lopreato 1994; Degler 1991; Marsland and Leoussi 1996; Sanderson 2001, p. 136). I will not go into this discussion, but focus instead on the possible relevance of an evolutionary psychological perspective for sociology. I then elaborate on the objective of this study in light of two persistent criticisms of evolutionary approaches to human behavior.

4.1 What is the relevance of evolutionary psychology to sociology?

Many non-sociologists, as well as sociologists who embrace an evolutionary perspective, have tried to persuade sociologists of "the need for Darwin" (for references, see Lopreato and Crippen 1999). For example, Nielsen (1994) identifies three domains in which evolutionary psychology might contribute to sociology: sex and gender, collective action, and human nature. Lopreato and Crippen (1999) make a similar case for the subjects of sex differences, relations between the sexes,

ethnocentrism, and social stratification. Studies by Wielers and de Vos (1999) and by Kanazawa (2001) offer improvements to rational choice theory that focus on the importance of emotions and the explication of the goals humans pursue. Sanderson (2001) presents a "unified theory of human society," which seeks to show that the basic principles of sociobiology are highly compatible with some traditional models of social theorizing (p. 143). De Vos (2004) argues that sociological concepts of community could profit greatly from grounding in modern insights about human social nature.

Either implicitly or explicitly, all of these scholars criticize sociologists for ignoring the biological nature of humans and claim that sociological theories would benefit from paying more attention to the evolved psychological mechanisms with which the human brain is equipped. Pinker (2002) refers to the denial of human biological nature as *blank slateism*. Cosmides and Tooby (1992) consider it the primary characteristic of their conception of the *Standard Social Science Model*. According to this model, humans have been able to transcend their biological tendencies, due to their cognitive capabilities. They have developed a capacity for culture and learning that makes them boundlessly flexible. At birth, the human mind is a "blank slate" that must be filled with knowledge about the world and how to behave. This knowledge is assumed to be acquired from the social and cultural environment.

The blank slate assumption has been influential in the social sciences, particularly in the 1920s to 1960s. Sociology, cultural anthropology, and psychology were all permeated with the idea that humans are products of their (social) environments or their cultures. In sociology, the feminist idea prevailed that typical feminine and masculine behaviors can be explained completely by environmental inputs. According to this idea, baby boys differ from baby girls only in their genitals. This difference leads parents to raise their sons and daughters differently, with the result that men become more aggressive, assertive, and interested in sex, while women become more caring, empathic, and coy in sexual affairs (e.g., Fausto-Sterling 1985). Cultural anthropology was characterized by a strong cultural deterministic tradition. This was most evident in the work of Margaret Mead, whose famous description of Samoan society as a society whose attitudes toward sex were much more relaxed than those of Western society (e.g., girls could engage in exploratory sex before marriage and violent rape was non-existent) was used as the ultimate proof that different cultures are infinitely variable. Finally, the behaviorist tradition in psychology assumed the environment to play an exclusive role in shaping human (and animal) behavior. According to this perspective,

selective reinforcement could be used to form associations between any given stimulus and any behavioral response.

All of the traditions described above have been severely criticized. The notion that sex differences are determined socially has been falsified by a number of "natural experiments" in which biological boys were raised as girls because of disease or accident. The "girls" in all of these cases turned out to be strongly masculine (Colapinto 2000; Reiner et al. 2004). Furthermore, the likelihood that the behaviors of genetically neutral children, who have female body plans, and are therefore usually raised as girls, will be more characteristically feminine or masculine depends on whether they received their single X-chromosome from their mothers or from their fathers (Skuse et al. 1997; for further references, see Campbell 2002). Second, the idea that different cultures are infinitely variable, as implicated by the cultural deterministic tradition in anthropology, has been falsified as well. Critics have demonstrated that Mead's conclusions were strongly biased, and that Samoan culture was sexually no more relaxed than any other society (e.g., Freeman 1998). More generally, there are numerous attributes that are universal: in all cultures humans use spoken language, live in groups, are interested in sex, have coyness displays, care for their children, compete for status, prefer ingroup members to outgroup members, have childhood fear of strangers, gossip, cry, make jokes, insult each other, have myths, dance, make music, have beliefs about death, have a division of labor, et cetera (for a list of human universals, see Brown, 1991). Finally, the environmental determinism that is inherent in the behaviorist tradition implies that there are no restrictions concerning the content or timing of things that are to be learned. Numerous studies have suggested that learning is not global, but biologically constrained (Klein and Mowrer 1989). For example, rats easily learn the connection between drinking a specific substance and (X-ray invoked) nausea, but they have much more trouble learning the connection between drinking a specific substance and flashing lights or noise (Garcia and Koelling 1966; for a review of related experiments, see Logue 1988). Moreover, although human babies are extremely flexible in learning language, this ability to learn disappears once a "critical period" has elapsed (Cummins and Cummins 1999). I return to the issue of the limits of learning in Section 4.2.1.

There is also a fundamental problem with the perception of humans as blank slates. As I argued in the discussion of the darwinian anthropological concept of humans as fitness maximizers, learning adaptive behavior through trial and error is impossible in the presence of an endless number of possible cues and responses. Chomsky (1980) made a similar point in the proposition that humans are endowed with a Universal Grammar. Given that the spoken language children

hear from their parents could be compatible with an infinite number of possible grammars, the only possible explanation for the fact that children succeed in learning the correct grammar is that they have an innate language device. In its most basic form, the argument holds that there can be no learning without an innate circuitry to do the learning (Pinker 2002, p. 35). A "blank slate" will stay forever blank (Cosmides and Tooby 1995, p. 45).

Although the influence of the social and cultural deterministic traditions has faded in psychology and cultural anthropology, it has not happened in sociology (Lord and Sanderson 1999; Lieberman 1989; Sanderson and Ellis 1992). Most sociological textbooks still insist on the separation of culture and biology (e.g., Bruce 1999; Tischler 1993).

4.2 Criticisms of evolutionary approaches to human behavior

This section elaborates on what the objective of this dissertation is, and, more importantly, what it is not. I present this elaboration in light of two persistent criticisms of evolutionary approaches to human social behavior that are shared by many sociologists: the criticism that such studies amount to genetic determinism, and the criticism that they are nothing but "storytelling."

4.2.1 Genetic determinism

The first criticism concerns the idea that evolutionary approaches to human behavior amount to genetic determinism (e.g., Bleier 1984; Freese 1994; Lewontin 1979; Rose et al. 1984; Rose 1978). In its most extreme form, this criticism holds that evolutionary psychologists (and other proponents of evolutionary approaches to human behavior) claim that we are fully driven by our genes, with environmental factors having no influence at all; people are born with a set of genes that determine their preferences, personalities, and behavioral tendencies. There are genes that make some people helpful and genes that condemn others to lives of criminality.

This dissertation seeks to test evolutionary hypotheses concerning reciprocal altruistic behavior and emotions in humans. Making evolutionary claims about reciprocal altruism implies that there must be a genetic origin of reciprocal altruism. However, I do not claim that reciprocal altruistic behavior is the result of a *single gene*, nor do I wish to show that reciprocal altruistic behavior is *exclusively* governed by genetic factors. Both issues are discussed next.

No genes for scorekeeping and bonding behavior

Although a claim that a behavior has evolutionary origins presupposes a genetic basis, I am not investigating whether there exists a "bonding gene" or a "scorekeeping gene." First of all, it should be emphasized that investigating the link between genes and behavior is the domain of behavioral and developmental genetics. Studies in these fields (e.g., experiments involving artificial selection and studies assessing the degree to which behavioral characteristics are similar among fraternal and identical twins) provide ample evidence that such a link exists (Alcock 2001).

Given the work of behavioral and developmental geneticists, it would be unrealistic to postulate genes for such complex behaviors as bonding or scorekeeping. Genes are segments of DNA coding for specific enzymes. Enzymes produce specific biochemical reactions that might affect the development or operation of hormonal, muscular, or nervous systems. This may result in specific behavioral tendencies *in certain environments*. When behavioral geneticists announce the discovery of a gene for drinking behavior, smoking, anxiety, or anti-social behavior, it does not mean that they have found some kind of directive, written in the genes, which condemns the bearer to a life of drinking, smoking, anxiety, or anti-sociality. It means, rather, that possession of a particular gene produces different biochemical pathways, which, under certain environmental conditions, translates into behavioral differences, compared to individuals who do not have the gene (Alcock 2001; Bailey 1998; Barash 2001, p. 28).

Moreover, even if it were our goal, it would be impossible to pinpoint the genetic basis of scorekeeping or bonding behavior. This dissertation, as well as the majority of evolutionary psychological research, focuses on behavioral designs that were favored to such a high degree in the ancestral environment that they are now present in all "normal" members of the human species (Alcock 2001, p. 42; Bailey 1998; Cartwright 2001, p. 71; Tooby and Cosmides 1990a). Just as few humans lack the correct genetic make-up for having eyes, there are also few humans who lack the genetic make-up for reciprocal altruistic behavior. In the absence of genetic variation of a trait, it is impossible for behavioral geneticists to pinpoint the relevant genes (Bailey 1998, p. 212).

Beyond nature-nurture

By formulating evolutionary hypotheses about scorekeeping and bonding behavior, I do not claim that these behaviors are due entirely to genetic factors and that environmental, social, and cultural factors play no role. Many scholars have tried to

show that the rigid distinction between "nature" and "nurture" makes no sense (for example, see Ehrlich 2000; Pinker 2002; Ridley 2003). Genes and environment are inextricably intertwined in shaping human behavior. In different environments, a single gene may translate into different behavioral tendencies, or it may not be expressed at all. For example, a gene that produces a quick break-down of a neurotransmitter responsible for feelings of excitement and arousal might result in a criminal career for one person and a career on Wall Street for another.

The exact ways in which environment and biology interact to produce behavior is still a matter of discussion (for a review, see Janicki and Krebs 1998). In the *meme perspective*, culture and biology are completely independent (Dawkins 1989, p. 191). Their tremendous capacity for learning allows humans to imitate all types of behavior, both adaptive and inadaptive. Dawkins (p. 198-199) gives the example of celibacy: the cultural behavior of celibacy is extremely inadaptive, as it constrains individuals from reproduction. This is, however, exactly what makes it a very successful *meme*: because celibate people do not "waste" their time in efforts to reproduce, they have plenty of opportunities to spread the meme to other individuals. In the end, however, biological evolution always triumphs over memetic evolution; the absolute peak of the success of the celibacy meme would inevitably mark its downfall, because in the absence of newly born humans, the meme would become extinct.

In stark contrast to the meme view is the idea that culture is a tool for maximizing fitness. According to this view, humans have evolved a capacity for culture that enables them to track the environment, making adaptive adjustments to their behavior – both consciously and unconsciously – as conditions change (Alexander 1979; Irons 1979). This view is most prevalent among darwinian anthropologists, who assume that humans behave in such a way as to maximize their current fitness. As mentioned before (see Section 2), this idea contradicts both assumptions of evolutionary psychology (i.e., that humans are equipped with domain-specific psychological mechanisms and that these psychological mechanisms are adapted to ancestral conditions).

At present, most evolutionary psychologists adhere to a more moderate account of the interaction of environmental and biological factors. In this view, the structure of our brains makes it easier to learn some behaviors than it is to learn others. Drawing upon classical conditioning studies, Seligman (1970, 1971; see also Marks 1987) suggested that organisms are *more prepared* to learn fear responses to classes of objects that may threaten their survival than they are to learn such responses to non-threatening objects. The finding by Garcia and Koelling (1966; see also Garcia et al. 1989) that rats have more trouble learning the connection

between food tastes and flashing lights or noises than they have in learning the connection between food tastes and nausea (see Section 4.1), can thus be interpreted as evidence that rats are innately pre-programmed to form adaptively relevant associations more easily than adaptively irrelevant associations. A similar *preparedness* to link the eating of a specific food with nausea has been shown in humans (e.g., Logue 1988). Furthermore, Öhman and Dimberg (1978; see also Öhman 1985) have shown that negative facial expressions (pictures of angry faces) are more easily associated with electrical shocks than are positive or neutral facial expressions. In summary, organisms seem to have a biological preparedness to very quickly develop specialized cognitive functions for solving classes of problems that were critical to the survival and reproduction of their ancestors (cf. Ariew 1996; Cosmides and Tooby 1995; Cummins and Cummins 1999, p. B45).

It is important to stress that evolutionary psychologists do not claim that individuals are *only* able to learn behaviors that are (or were) adaptive, and avoid behaviors that are (or were) inadaptive. On the contrary, humans owe their dominance over the world to their extraordinary capacity to learn. The argument implies only that it takes more time and effort to learn behaviors that were inadaptive, or adaptively insignificant, in the past (de Vos and Wielers 2003, Papineau 2000). Thus, human children can be taught to eat both sweet and bitter foods, even though the perception of bitterness evolved to warn us that some foods were poisonous. Individuals can learn to drive cars and computers, even though cars and computers have not yet existed long enough to play any role in the process of natural selection. And, as speculated in Section 3.4, humans can learn to function in market societies by learning scorekeeping behavior.

However, although human children can be taught to eat (and to like) Brussels sprouts, it takes more trouble than it does to teach them to like apple pie. Similarly, humans can learn to drive cars and use computers, but it takes a considerable amount of practice. And finally, although humans can learn to keep score, it takes little more than a few positive interactions for business partners to be perceived as friends, resulting in bonding behavior.

4.2.2 Storytelling

A second criticism of evolutionary approaches to human behavior is that the focus on explaining behavior in terms of the benefits to individual survival and reproduction leads evolutionary psychologists to invent evolutionary explanations for *all* behaviors. This is expressed in criticisms concerning ad hoc explanations and *just-so stories*. In its most extreme form, this critique argues that evolutionary

researchers just pick an empirically founded fact and provide it with an interesting evolutionary explanation – the more ingenious the better (Gould 1978a; Kitcher 1985). A related criticism is that evolutionary researchers use tautological arguments, "explaining" a specific behavior by referring to empirical evidence for the prevalence of this behavior and concluding that people exhibit the behavior because it is (or was) adaptive (e.g., Freese 1994; Lindenberg 1999a, p. 407; Maryanski 1994).

The hypotheses offered in this dissertation are neither unfalsifiable nor tautological. Assuming that proximate mechanisms of reciprocal altruism evolved in the Pleistocene environment, I speculate that, in this environment, a bonding mechanism would have been more conducive to individual fitness than a scorekeeping mechanism would have been. I subsequently predict that many instances of reciprocal altruism can be more accurately described by a bonding mechanism than by the conventional scorekeeping mechanism, and that the bonding mechanism is more biologically prepared than is the scorekeeping mechanism.

Many potential outcomes could falsify these hypotheses. For example, the finding that people do not exhibit bonding behavior in conditions that are most similar to the ancestral environment would falsify the hypothesis that bonding is an evolved psychological mechanism. In addition, the finding that people are much more easily induced to perform scorekeeping behavior than they are to perform bonding behavior would falsify the hypothesis that bonding is the primary mechanism underlying reciprocal altruism. The hypotheses formulated in this dissertation can therefore not be written off as instances of "storytelling."

The criticism of tautology has also been raised against the theory of evolution in general. It based on a misunderstanding of the phrase "survival of the fittest." As long as fitness is determined independently from survival, there is no tautology (Gould 1977; 1989, p. 236). When providing an ultimate explanation of a behavioral tendency, it does not suffice to say that organisms behave in such a way because it is (or was) adaptive. Instead, we must explain *why* it is (or was) adaptive. As are most evolutionary psychological hypotheses (see for references Buss et al. 1998), my predictions concerning the bonding mechanism are based on an analysis of the conditions in the Environment of Evolutionary Adaptedness, which specifies *why* particular behaviors increased reproduction and survival under these conditions. For this reason, the criticism of tautological reasoning also does not hold.

5 Design of this dissertation

Because each of the chapters in this dissertation was written as a separate article, there is some overlap. All of the chapters focus on the distinction between the conventional scorekeeping mechanism and the relatively new concept of a bonding mechanism. To recapitulate, the primary goal of this dissertation is to investigate whether the scorekeeping mechanism is as ubiquitous as evolutionary psychologists generally assert. At times, I go a step further and address the question of whether the bonding mechanism is more biologically prepared than is the scorekeeping mechanism. Finally, I focus on emotions as intermediators between adaptation-relevant cues and behavioral responses.

Chapter 2 takes a closer look at the mechanisms underlying food sharing among hunter-gatherers, who live in conditions that are most similar to those of our ancestors and who are therefore the most suitable candidates for providing evidence of ancestrally evolved psychological mechanisms. Anthropologists have conducted many studies on food sharing. Chapter 2 scrutinizes those studies for their potential support to either bonding or scorekeeping mechanisms.

Chapter 3 is a simulation study, investigating the relative success of a strategy based on the scorekeeping mechanism (called "Keeping Books Balanced") and a strategy based on the bonding mechanism (called "Commitment"). The primary aim of this chapter is to show that the conventional scorekeeping strategy owes its popularity to its success in the context of a Prisoner's Dilemma environment. In the context of an environment that more closely resembles the EEA, (i.e., where actors get in need of help in an unsystematic and unpredictable way), and in which they must select their interaction partners rather than having them assigned externally, a scorekeeping strategy is expected to perform worse than a bonding strategy.

Chapters 4 and 5 address the question of how those psychological mechanisms work. Chapter 4 focuses on the relation between cues and behavioral responses, while Chapter 5 centers on the role of emotions. Both studies are based on scenario data. Subjects were asked to imagine a situation in which they are indebted to another person, or in which another person is indebted to them. The scenarios were constructed in such a way as to pose a dilemma between bonding and scorekeeping. As a result, a subject's behavioral response was indicative of either scorekeeping or bonding behavior. Chapter 4 is closely related to social psychological studies on communal and exchange relationships, as it focuses on the effects of situational characteristics that are typical for either communal or exchange relationships. This was done by varying the object of help (either

assistance in the case of illness or lending money) and the relationship with the other person (either a good friend or an acquaintance). Finally, by using an implicit prime the chapter also includes an attempt to test the speculation that bonding is an evolved psychological mechanism, while scorekeeping is not.

Chapter 5 focuses on the role of emotions in the bonding and scorekeeping mechanisms. It addresses both the question of which emotions are associated with the bonding mechanism and which emotions with the scorekeeping mechanism and the question of the extent to which emotions play an intermediating role between cues and behavior.

Finally, Chapter 6 summarizes the preceding chapters, draws conclusions concerning the research questions, and considers recent developments and suggestions for future research.

CHAPTER 2

Scorekeeping or bonding? What do studies on hunter-gatherer food sharing tell us about proximate mechanisms of reciprocal altruism?[1]

1 Introduction: scorekeeping and bonding mechanisms of reciprocal altruism

Do individuals help others at a cost to themselves? This question – the question of altruism – has been considered of major importance in sociobiology and evolutionary psychology (Hamilton 1964; Trivers 1971; Wilson 1976, p. 3). In his seminal article, Trivers (1971, p. 35) defined altruism as "behavior that benefits another organism, not closely related, while being apparently detrimental to the organism performing the behavior, benefit and detriment being defined in terms of contribution to inclusive fitness." In the same paper, he introduced the concept of reciprocal altruism, arguing that providing a benefit to a non-related individual will be beneficial to an actor's fitness *if the costs of this action are lower than the benefits received back in the long term*. Individuals who are willing to provide benefits to non-related others are better off on the long run than individuals who reap the benefits of altruistic others' without bothering to reciprocate, *provided that the altruist responds to the cheater by curtailing all future possible altruistic gestures to this individual* (Trivers 1971, p. 36). In sum, according to the notion of reciprocal altruism, individuals will only help others at a cost to themselves if they get something in return.

Trivers' concept of reciprocal altruism has been quite influential. Evolutionary game theorists have modeled reciprocal altruism as a strategy in the

[1] This chapter has been submitted for publication.

iterated Prisoner's Dilemma game.[2] In his computer tournaments, Axelrod (1984) had actors with different strategies compete in iterated Prisoner's Dilemmas. The most successful strategy was a very simple one called Tit-for-Tat (TFT). TFT was described as a nice, but retaliatory strategy: it cooperates on the first move and thereafter imitates the move of its interaction partner, rewarding cooperative behavior with cooperation and retaliating defecting behavior with defection. Following Axelrod's tournaments, many mathematical and simulation studies have been conducted with other payoff matrices, additional parameters, large groups instead of dyads, different strategies et cetera (Boyd and Richerson 1988; 1989; Hayashi 1993; Kollock 1993; Nowak and Sigmund 1993; Roberts and Sherrat 1998). All of these studies agreed that, by the nature of the game, actors would only be able to withstand non-cooperative strategies if they made their behavior *conditional* on the behavior of their interaction partners, that is, by behaving according to some form of TFT-strategy or by *keeping scores* with regard to each other's contributions (Brown 1983; Dugatkin 1997).

The concept of reciprocal altruism also plays a major role in the field of evolutionary psychology. According to evolutionary psychologists, our human ancestors developed mental modules, or proximate mechanisms, in order to respond to the specific adaptive problems which they faced on the Pleistocene savanna (Tooby and Cosmides 1990b). In general, savanna environments are characterized by seasonality and patchily distributed food resources (Folch and Camarasa 2000, p. 20; Foley 1993; Kurland and Beckerman 1985; Tooby and DeVore 1987, p.223-224). As a consequence, food resources are acquired asynchronously, sporadically and unpredictably (Barret et al. 2002, p. 72; Foley 1987; Kurland and Beckerman 1985, p. 80). In such conditions, reciprocal sharing of food is supposed to have been adaptive, since it reduces the risk of starvation (Boyd and Silk 1997; Campbell 1979; Kurland and Beckerman; Winterhalder 1986). Furthermore, since meat often comes in large quantities in excess of what the

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[2] The Prisoner's Dilemma is a game in which two players have to choose between cooperating (C) or defecting (D). Players receive payoff dependent on both their own move, and that of the other player (see figure; Ego's payoff is mentioned first), with T>R>P>S and T+S < ½R. If the game is played only once, each individual player benefits more by defecting, regardless of what Alter does, resulting in a collectively suboptimal outcome. In an iterated game, cooperative players can do better than defectors, provided that the number of interactions is large enough. (see Axelrod 1984; Luce and Raiffa 1957).

		Alter C	Alter D
Ego	C	R,R	S,T
	D	T,S	P,P

capturers can readily consume, it is a suitable object of sharing (De Waal 1996; Isaac 1978; Potts 1984; Tooby and DeVore, p. 224). Individuals engaging in the mutual sharing of food, therefore, were probably better off than were individuals who did not. Since unconditional sharing would make them highly vulnerable to free-riders, who would beg for food but never give something in return, selection pressure was strong to avoid being exploited. The most obvious mechanism for avoiding exploitation would be some variation on the TFT-strategy, that is, a mechanism that induces individuals *to keep track of the amount of benefits provided and benefits received, and only to give food to another individual if this does not result in a misbalance of books*. I use the term scorekeeping reciprocity for such behavior, and scorekeeping mechanism to denote the proximate mechanism responsible for this behavior.

The most extensive elaboration of a scorekeeping mechanism is Cosmides and Tooby's study of cheater detection (Cosmides 1989; Cosmides and Tooby 1990; Cosmides and Tooby 1992). In order to find out if humans are equipped with a proximate mechanism for detecting situations in which a person accepts benefits without giving anything in return, they tested whether subjects are better at detecting violations of logical arguments involving the violation of a social contract than those involving violations of descriptive rules (Cosmides 1989; Cosmides and Tooby 1992; Gigerenzer and Hug 1992). Their results showed that this is indeed the case.

Although scorekeeping is often considered as *the* proximate mechanism of reciprocal altruism (Brown 1983; Cosmides and Tooby 1989, p. 57; Cosmides and Tooby 1992, p. 176; Dugatkin 1997, p. 39; Gigerenzer 1997, p. 274), several studies have criticized the focus on avoiding exploitation. This focus has diverted attention from another aspect of mutual sharing which is at least as important, namely the *willingness to cooperate* (De Vos et al. 2001; Kiyonari et al. 2000; Tooby and Cosmides 1996). Furthermore, several studies have noted the importance of commitment, friendship, and a need to belong for reciprocal altruistic behavior (Baumeister and Leary 1995; Caporael et al. 1989; De Vos et al. 2001; Tooby and Cosmides 1996). Thus, an alternative option is a mechanism which is not primarily concerned with avoiding to be exploited but with *providing help to one's friends or group members if there is a need*. Such a mechanism might have its origins in much older neuroendocrine mechanisms for parental care that have extended as to include also caring for individuals not closely related (Bell 2001; Carter 1998; Eibl-Eibesfeldt 1989, p. 169-70; Panksepp 1998; Stevens and Price 1996, p. 14).

At first glance, a mechanism for reciprocal altruistic behavior without a focus on avoiding to be exploited, seems implausible to have been selected.

However, many examples show that proximate mechanisms need not be linked to their ultimate functions in a straightforward way (Brosnan and De Waal 2002; Caporael et al. 1989; Gurven [in press]; Tinbergen 1963). For example, Konrad Lorenz showed that newborn geese and ducks are *imprinted* to follow the first moving object they encounter after hatching. In general, this will be their parent, but imprinting also occurs towards human beings and inanimate objects (Lorenz 1988; see also Jaynes 1957; Hoffman 1996). Obviously this makes them very vulnerable to predators: it would have been much more adaptive if they would only follow their own parent and flee from any other individual, or at least from any other individual measuring more than twenty times their size. Apparently, the tendency to follow the first moving object after hatching has had sufficient fitness benefits, compared to fitness costs, to have been selected as a proximate mechanism to serve the relevant *ultimate function* – protection. Similarly, Trivers' conjecture that helping behavior has evolved because the costs of helping are lower than the benefits on the long run, refers to the ultimate function of reciprocal altruism. The proximate mechanism that has evolved to actually conduct this function does not necessarily involve keeping track of costs and benefits. If a mechanism for providing (unconditional) help to a friend or group member can be shown to have had sufficient fitness benefits in the ancestral environment, compared to its fitness costs, it is a plausible mechanism of reciprocal altruism.

Taking into account the evolutionary history of our hominid ancestors, the fitness costs of such mechanism may have been lower than expected. First, groups were small and composed of several nuclear families (Barrett et al. 2002; Power 1988; Rodseth et al. 1991), so the *benefits of free-riding* would have been relatively low. The chances of exploiting one's own sibling, cousin, reproductive partner, sibling's or cousin's reproductive partner, reproductive partner's sibling or cousin et cetera, would have been high. Second, in conditions in which individuals are highly dependent on each other - like in the savanna environment – the *potential costs of free-riding* are high. On two levels, selection may impede the success of free-riders. First, free-riding might be selected against on the level of the individual. Since groups were small, free-riding would not go unnoticed. In an environment in which one cannot survive on one's own, the costs of falling out of favor and losing all one's reciprocity-partners are extremely high and they probably counterbalance the benefits of free-riding (Tooby and Cosmides 1996; Yamagishi et al. 1999). Second, on the group level free-riding is definitely selected against. Groups comprised of uncooperative individuals have a higher probability of going extinct than groups comprised of altruists. Because the effect of such between-group selection is generally overridden by the individual benefits accruing to free-riders, group

selection is commonly considered as improbable, if not impossible. Under some conditions, however, the effects of between-group selection have been shown to be stronger than the effects of within-group selection (Wilson and Sober 1994). If groups are demographically closed, or have low phenotypic variation, for example because individuals tend to imitate or conform to the behavior of the majority, and if competition between groups is high, or groups run a high risk of going extinct, groups of mainly cooperative individuals outrun groups containing mainly free-riders. It is not implausible that these conditions applied to the hominid groups in the ancestral environment (Boehm 1999; De Vos et al. 2001; Fehr and Fischbacher 2003; Gintis 2000; Gintis et al. 2003; Richerson and Boyd 1998).

There is also a clear *benefit* to a mechanism for providing help to one's friends or group members if there is a need, compared to a scorekeeping mechanism. Scorekeeping is a useful strategy in a situation in which interaction partners call upon each other in a predictable, systematic way. The exemplary model of such a situation is the delayed Prisoner's Dilemma, in which two actors take turns in deciding whether they cooperate or defect. In the Pleistocene savanna environment, however, the acquiring of food, and consequently, the ability to share with others, was everything but predictable (Barret et al. 2002, p. 72; Kurland and Beckerman 1985). An individual who would keep score of his own and his interaction partner's provided benefits, and who would avoid giving benefits if the other was in his debt, would run the risk of losing committed interaction partners. In other words, "the ability to attract assistance during such threatening reversals in welfare, where the absence of help might be deadly, may have had far more significant selective consequences than the ability to cultivate social exchange relationships that promote marginal increases in returns during times when one is healthy, safe, and well-fed" (Tooby and Cosmides 1996, p.132). Because of the focus on commitment and care towards those who are close, I use the term *bonding mechanism* to denote this mechanism.

Nevertheless, the idea that reciprocal altruism in humans takes the form of scorekeeping is clearly the most popular. In many studies, food sharing in hunter-gatherers is used as the key example of scorekeeping reciprocity (see for example Cosmides and Tooby 1992; Gigerenzer 1997; Pinker 1998; Ridley 1998). In general, since living conditions in hunter-gatherer and horticulturalist societies most closely resemble the environment inhabited by our ancestors, postulations of innate traits or evolved mechanisms gain credibility if they are backed up by empirical evidence from anthropological studies. However, the question of whether hunter-gatherer food sharing practices provide unequivocal support to a scorekeeping mechanism of reciprocal altruism has not been addressed. The aim of this article is to review

anthropological studies on food sharing and determine the extent to which they provide support to either scorekeeping or bonding reciprocity.

2 Expected sharing behavior based on scorekeeping and bonding mechanisms

What patterns in sharing behavior among extant hunter-gatherers would provide support to the scorekeeping mechanism and bonding mechanism, respectively? As the scorekeeping mechanism has originated in selection pressures concerning the potential exploitation by free-riders, one would expect the giving of food to be primarily guided by the avoidance of misbalances in the amount of benefits received and the amount of benefits provided. Sharing relationships should be *balanced*, and the providing of food should be *contingent* upon the receiving of food (Bliege Bird et al. 2002, p. 298; Gurven et al. 2001, p. 275; Hawkes et al. 2001). Thus, individuals try to repay those who have provided them with food, and individuals who have given food expect to receive food in turn. Providers of food are concerned with not being exploited, and will refrain from giving to individuals who have not repaid them (Bliege Bird et al. 2002; Gurven et al. 2000a). Conversely, receivers of food are concerned with not being considered as free-riders and do their utmost to pay off their debts (Hawkes et al. 2001; Kaplan and Hill 1985a).

In contrast, if food sharing is guided by the bonding mechanism, one would expect sharing behavior to be guided by need rather than the avoidance of misbalances in benefits received and benefits provided. If an individual has failed in acquiring food, provided that the group is small enough to mirror the group size in the ancestral environment, group members will give him food regardless of whether he is in their debts. In larger groups, in which it is impossible to have close relationships with all group members, individuals will perform bonding behavior towards a limited number of "friends", while there will be no or hardly any sharing with those outside the group of friends.

The distinction between these two mechanisms of sharing behavior is not new. Sahlins (1972) distinguished between generalized reciprocity on the one hand and balanced reciprocity on the other. These two types of reciprocity have similarities with the bonding and the scorekeeping mechanism, respectively. *Generalized reciprocity* is defined as solidary transactions in which the material side of the transaction is repressed by the social side: reckoning of outstanding debts cannot be overt and is typically left out of account. Although there is an obligation

to repay, this obligation is diffuse, and dependent on the need of the original donor and the ability of the original recipient (Sahlins 1972, p. 193-194). *Balanced reciprocity*, in contrast, is characterized by an intolerance of one-way flows. The material side of the transaction is at least as critical as the social: there is more or less precise reckoning, as the things given must be covered within some short time (p. 195).[3] Sahlins' distinction is similar to Malinowski's distinction between *pure gifts*, in which an individual gives an object or renders services without expecting or getting any return (Malinowski 1922, p. 177), and *pure trade*, which is characterized by the element of mutual advantage: each side acquires what is needed and gives away an article less useful to him but equivalent in value (p. 189). Between these two extreme cases, Malinowski discerned a number of intermediary forms of exchange.

These traditional accounts are not based on evolutionary arguments. Rather a structural-functionalist argument is used: reciprocity is considered an instrument for maintaining stability in society (Malinowski 1926; Mauss 1954; Sahlins 1972). Furthermore, both Sahlins and Malinowski considered the generalized and balanced reciprocity as complementary patterns. Generalized reciprocity or pure gift giving was situated within the realm of kin relations. With increasing social distance, reciprocity was supposed to become less generalized and more balanced or trade-like.

3 Two anthropological traditions

Anthropological studies on food sharing can be categorized into two traditions: more traditional cultural anthropological studies on the one hand and evolutionary anthropological studies on the other hand. I will start by brieafly introducing both traditions, focusing on the differences between them. Next, I will consider the evolutionary anthropological tradition in some more detail, discussing the different models that might explain food sharing.

3.1 Cultural versus evolutionary anthropology

Cultural anthropological and evolutionary anthropological studies differ both in theoretical background and research methodology. Cultural anthropological studies generally use qualitative research methods, providing descriptive reports of the

[3] Sahlins also distinguished a third kind of reciprocity, termed "negative reciprocity": *the attempt to get something for nothing*. (Sahlins 1972, p. 195)

objects of their research. It is not surprising, therefore, that in most studies, reciprocity is defined in terms of the *rules or motivations* for sharing, offered by the individuals under study themselves. In contrast to the structural-functionalist argument to explain the existence of reciprocal altruism, present in some early cultural anthropological works (Malinowski 1926; Mauss 1954; Sahlins 1972), most later cultural anthropological studies on reciprocal altruism and food sharing use the argument of risk-reduction, which is also present in the evolutionary anthropological studies. Since even the best hunters face a high risk of failing in capturing game, every day chances are considerable that a family will not obtain enough food resources (Altman 1987; Barret et al. 2002, p.72; Bliege Bird and Bird 1997, p. 50; Cashdan 1985; Hawkes et al. 2001, p. 115; Kaplan and Hill 1985a, p. 227; Kurland and Beckerman 1985; Marshall 1976; Wiessner 1982). The functional argument is still present, however, in the reasoning that hunter-gatherers pool resources and practice band-wide sharing *because such a system is to the advantage of all.* Thus, reciprocal food sharing is considered some kind of collectively achieved solution to reduce the variance in resource acquisition (see for examples of such a functional argument Aspelin 1979, p. 324; Balicki 1968, p. 81; Marshall 1976, p. 295). Evolutionary anthropologists have dismissed this argument as being a good-for-the-species-argument: although pooling of resources and band-wide sharing is beneficial to the group, every individual is better off if he refrains from sharing (Blurton Jones 1984; Kaplan and Hill 1985a; Peterson 1993; Smith 1988). Although some cultural anthropological studies acknowledge that persons who are unwilling to share are subject to social control through gossip, ridicule and ostracism, and persons who feel exploited may cease to produce for a while and force others to do their share (Boehm 1999; Harris 1980, p. 228; Wiessner 1996, p. 186), in general the problem of free-riders receives little attention. As a consequence of the functional argument, the picture of sharing patterns given by most cultural anthropological studies, is one which closely resembles Sahlins' concept of generalized exchange.

In contrast, evolutionary anthropological studies try to explain food sharing by models based on evolutionary theory. Applying models from biology and economics, mainly quantitative research methods are used. The results of cultural anthropological studies are criticized as being merely anecdotal and fallible to ethnographer's impressions (1993a, p. 707-708; Hill and Kaplan 1993, p. 703). Moreover, evolutionary anthropologists are primarily interested in *ultimate* explanations for food sharing behavior, rather than in the *proximate* explanations that are present in cultural anthropological studies (Blurton Jones 1987; Feinman 1979; Kaplan and Hill 1985a). Evolutionary anthropologists assume that humans

are capable of adapting their strategies to environmental conditions, in this way maximizing their inclusive fitness (Blurton Jones 1984; Smith, Borgerhoff Mulder, and Hill 2001; Turke 1990). This implies that they will perform behavior that yields the highest benefits and involves the lowest costs. In contrast to the functional argument present in many cultural anthropological studies, evolutionary anthropologists argue that individuals will only share food in those conditions in which it serves their inclusive fitness.

3.2 Evolutionary anthropological models of food sharing

The most prominent model used to explain food sharing patterns is Trivers' model of *reciprocal altruism* (Trivers 1971). In addition, evolutionary anthropologists also use Hamilton's model of *kin selection* (Hamilton 1964), Blurton Jones' *tolerated theft model* (1984, 1987) and various models of indirect reciprocity (Alexander 1987; Hawkes 1993b; see also Gurven [in press]). In the following section, each of these four models is introduced. Moreover, the relevance of each model for the question of whether sharing patterns can be explained by scorekeeping versus bonding mechanisms is discussed.

3.2.1 Reciprocal altruism

In line with the focus on ultimate explanations, evolutionary anthropologists have formulated and tested several hypotheses about the *conditions* under which sharing behavior occurs. Since the benefits of sharing food are highest in case of high variance in resource acquisition, *sharing should occur more when food units are large and unpredictably acquired* (Bliege Bird et al. 2002; Feinman 1979; Gurven et al. 2000b; 2001; Hames 1990; Kaplan and Hill 1985a). In general, the empirical evidence is in favor of this hypothesis. Large packages of food are shared more than small packages (Gurven et al. 2000b; 2001; Kaplan and Hill 1985a), and food items which are difficult to acquire are shared to a higher degree than food items that are easier to acquire (Bliege Bird and Bird 1997; Hames 1990; Kaplan and Hill 1985a; but see Bliege Bird et al. 2002).

More relevant to the issue of whether food sharing is governed by a scorekeeping or a bonding mechanism, are the hypotheses about the *behavioral patterns* with regard to sharing, as formulated by evolutionary anthropologists. Given the need to share food in order to be assured of receiving food from others when one has failed to acquire any, and given the presence of free-riders, they have

predicted a pattern of *balanced exchange*. An individual's act of sharing food with another individual should be *contingent upon* the amount of food received from this individual (Bliege Bird et al. 2002, p. 298; Gurven 2001, p. 275; Hawkes et al. 2001). Obviously, empirical support for contingent sharing would strongly favor the scorekeeping mechanism.

3.2.2 Kin selection

Since related individuals share part of their genes, under some conditions, an individual can be more successful in spreading his genes by acting in the interest of a relative than he can by acting in his own self-interest (Hamilton 1964).[4] Several studies have tested whether individuals provide more food to related than to non-related individuals, with varying results. Kaplan and Hill (1985a, p. 229; see also Kaplan et al. 1984) found no support for this hypothesis. Gurven and coworkers (2000b, p. 197; 2001, p.284) did find a significant bias in food transfers to kin-related individuals.

On itself, the kin selection model is not relevant to decide whether sharing patterns are best described as the result of a scorekeeping versus a bonding mechanism. The empirical observation that related individuals share more than non-related individuals does not favor one of either mechanisms, since both allow for different behavior towards kin. However, using the model of kin selection in combination with the model of reciprocal altruism, one would expect that non-related individuals are more preoccupied with maintaining a balance in benefits given to another individual and benefits received from this individual, than are related individuals, who are more tolerant of imbalances. Support for this hypothesis would favor the scorekeeping mechanism.

3.2.3 Tolerated theft

In contrast to the reciprocal altruism model, the tolerated theft model (Blurton Jones 1984; 1987; Kaplan and Hill 1985a) does not assume that individuals share in order to reduce the risk of starvation. Instead, it begins with the assumption that individuals will fight about a resource only if the benefits of keeping the resource exceed the costs of fighting (Parker 1974). Because the benefits of a large unit of

[4] More technically: providing benefits to other individuals at the expense of one's own fitness will be favored by natural selection if the ratio of fitness benefits to the receiver and fitness costs to the provider exceeds the inverse of their genetic relatedness ($B/C > 1/r$) (Hamilton 1964: Kaplan and Hill 1985a).

food follow a diminishing return curve (the larger the food item, the lower the fitness benefits of each additional kilogram), individuals will defend an acquired food resource only until they have consumed so much of it that the benefits of defending the rest of it would not exceed the costs. Thus, Blurton Jones (1984, 1987) suggested that food resources that are found sporadically, unpredictably and in large packages give rise not to *risk-reducing reciprocal altruism*, but to *tolerated theft*, with variance reduction of food intake being only a by-product (Blurton Jones 1987, p. 51).

The tolerated theft model has given rise to two hypotheses. First, in the case of strict tolerated theft, all members of a village or band should receive equal shares (Bliege Bird and Bird 1997; Gurven et al. 2001; Gurven et al. 2000b). A weaker version of this hypothesis is that food is not distributed throughout the entire band, but only to geographically close households, who cannot fail to notice when an acquired food item is brought in (Bliege Bird and Bird 1997, p. 60; Gurven et al. 2000b). The second hypothesis is that share size correlates with *recipient's need*. The rationale for this prediction is that an individual's need, operationalized by his family size, is proportional to the strength of the demand (Bliege Bird and Bird 1997, p. 60).[5]

Support for the tolerated theft model would favor the bonding mechanism rather than the scorekeeping mechanism – for two reasons. First, the model explicitly states that free-riders, and even fulltime scroungers, are tolerated by those who produce food (Blurton Jones 1987, p.45).[6] Second, predictions based on the tolerated theft model are empirically equivalent to the predictions following from the bonding mechanism. According to the tolerated theft model, individuals passively allow group members to take parts of the food resource, as long as it does not pay to oppose them. According to the bonding hypothesis, individuals actively give food to group members or friends, if there is a need. Provided that groups are small enough as to allow individuals to have close relationships with all group members, both models predict that shares are provided according to *need,* or

[5] A third hypothesis is provided by Kaplan and Hill (1985a), who were the first to derive hypotheses from the tolerated theft model. They predicted that individuals with greater fighting ability would receive more food than would weaker individuals. They found no evidence, however, that fighting ability, or resource-holding potential, had any effect on food sharing (Kaplan and Hill 1985a, p.231). In later studies, the tolerated theft model is not associated with differences in either resource-holding potential or fighting ability.

[6] These conditions lead to free-rider problems similar to those found in sharing situations: if foragers always do worse than scroungers, why would anybody be a forager? Blurton Jones (1987, p. 45) dealt with this problem rather unconvincingly by introducing a selection pressure for *persuading others to become a forager*.

that food distributions are *egalitarian*, that is, all group members getting *equal shares* (Peterson 1993; Woodburn 1982).

3.2.4 Indirect reciprocity

The indirect reciprocity model was introduced to explain acts of providing benefits which are not returned by the receiver. Providing benefits to an individual without getting anything in return is considered to be adaptive to the extent that observers reward the generous individual (Alexander 1987; Trivers 1971).[7] Evolutionary anthropologists have proposed at least two different models related to the concept of indirect reciprocity: the showing-off model (Hawkes 1993b; Hawkes et al. 2001) and the costly signaling model (Gurven et al. 2000a; Smith and Bliege Bird 2000, p.245). Although they use different theoretical arguments, proponents of both models expect successful and generous hunters to be compensated by rewards such as enhanced mating opportunities (Bliege Bird and Bird 1997, p. 63-66; Gurven [in press]; Hawkes 1993b, p. 349).

Empirical support for indirect reciprocity is not relevant to the opposition of scorekeeping versus bonding. By definition, the concept of indirect reciprocity implies that benefits are not returned by the receiver, but by others who have observed the generous behavior. The absence of a return benefit by the recipient, therefore, cannot be taken as an indication of free-riding.[8] Rather than mechanisms for scorekeeping or bonding, indirect reciprocity implies that sharing patterns are the result of mechanisms for seeking and responding to reputation and status. The number of studies testing for indirect reciprocity is quite low, however, and none of them show that sharing patterns can be *completely* accounted for by models of indirect reciprocity (see Bliege Bird and Bird 1997; Gurven et al. 2000b; Kaplan and Hill 1985a), so there is no reason to discard the mechanisms for *direct* reciprocity (such as the scorekeeping and bonding mechanisms).

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[7] References to indirect reciprocity avant-la-lettre can be found in earlier anthropological works. In 1951, Leach criticized the idea that transactions must be strictly balanced. Part of the balance might be in such *intangibles* as status or prestige (Leach 1951; see Pryor and Graburn 1980). Similarly, Dowling (1968, p.505) suggested that band-wide sharing by successful hunters might be motivated by the ambition of acquiring social esteem and influence.

[8] This point has been considered as a major weakness of the models of indirect reciprocity: if A shares food with B in order to be rewarded by individuals who have observed his generosity, a *second order collective good problem* arises: why should anyone repay a provider if he will receive an equal portion in any case? (Hill and Kaplan 1993, p.704; Smith 1993, p. 356).

4 Empirical tests of bonding

There are no studies explicitly testing the hypothesis that individuals respond to the needs of their group members or friends, regardless of misbalances in benefits provided and benefits received. There are some studies addressing the question whether sharing is egalitarian, whether need affects sharing behavior, and whether proximity affects sharing behavior. If sharing patterns result from a bonding mechanism, one would expect egalitarian sharing in groups small enough to enable close relationships between all group members. In larger groups one would expect individuals to restrict their sharing to a limited number of "friends". Finally, there should be a positive effect of one's need on the receiving of food. Thus, the following hypotheses can be derived.

1) Sharing patterns are egalitarian in relatively small groups.
2) In larger groups, individuals restrict their sharing to a limited number of "friends", while there will be no or hardly any sharing with those outside the group of friends.
3) An individual who is in need of food will receive food from his group members or friends.

4.1 Sharing patterns are egalitarian in relatively small groups

Several studies have tested the hypothesis of egalitarian sharing, that is, all families getting equal shares. This hypothesis follows both from the concept of generalized exchange as presented in the cultural anthropological studies, and from a strict version of the tolerated theft model. Thus, Aspelin (1979), in one of the earliest quantitative studies on food sharing, tested hypotheses about equality of sharing, and sharing as a response to need in Mamaînde horticulturalists and hunter-gatherers (Brazil). One of his predictions was that *the percentage of food a family receives* (y) depends on *the number of families present* (n) according to the function $y=1/n$. For example, when two families are present (one of which would be that of the distributor), each is expected to get one half of the distributed product. When three are present, each should get 1/3, et cetera (Aspelin 1979, p. 317). The results showed the expected curvilinear relation between number of families present and the average percentage of the total amount of food received by one family.

Gurven and his coworkers (2001, p. 281) used the tolerated theft model to formulate a similar hypothesis, namely that each household should receive a proportion of $1/n$ of each acquired food item, with n referring to the *total number of*

households in a village. Their data, collected among the Hiwi (Venezuela) and the Ache (Paraguay), did not support this hypothesis. Sharing breadth was relatively low, with an average of two to three families receiving shares from a single distribution (Gurven et al. 2000b, p. 188; 2001, p. 281). The different results of the Mamaînde study on the one hand (Aspelin 1979), and the Hiwi and Ache studies on the other hand (Gurven et al. 2000b, 2001) might be the consequence of the difference in the precise test (i.e., counting families present versus number of households in the village). An alternative explanation is that equal sharing only occurs in small groups: the Mamaînde village consisted of about ten nuclear families, whereas both the Hiwi and Ache settlements consisted of more than twenty nuclear families (Aspelin 1979, p. 113; Gurven et al. 2000b, p. 183; 2001, p. 277).

In addition, Bliege Bird and Bird (1997, p. 60) used the tolerated theft model to predict a positive correlation between the number of shares distributed and the number of potential recipients within a 100 meter-radius of the butchering household. This was confirmed by their data on turtle meat sharing among the Meriam (Melanesian Islands). Since this radius roughly corresponds to the size of a village district (p. 62), this result supports the hypothesis of equal sharing in small groups.

Finally, Kaplan and Hill (1985a) accompanied nine Ache foraging bands, consisting of 15 to 28 persons, on their foraging trips, ranging from 7 to 15 days (p. 228). Calculating the amount of calories produced and the amount of food eaten for all individuals, they did not find a significant correlation between these two variables. They concluded that Ache pool most of the food they acquire, and share food among families according to the number of families present (p. 233).

In addition to quantitative data on sharing patterns, descriptions of *the role of the hunter,* present in cultural anthropological studies, illustrate the focus on equality. In most cases described, hunters do not own the carcass and do not have any power over the food distribution (Endicott 1988; Marshall 1976; Wiessner 1996). They are expected to behave with modesty. Feelings of superiority as a consequence of skill in hunting are strongly curbed (Lee 1979; 1984, p. 440; Turnbull 1966). Thus, according to Wiessner (1996, p. 178-179)…

> (…) when a hunter is successful, he does not stride into camp and announce his kill, but leaves the carcass in the bush, slips in from the back of the hut, and sits unobtrusively by his fire. Others approach him and ask if he had seen any animals during his hunt. Even if his kill is large, he replies that he saw nothing of consequence while out hunting or that he killed only a small, scrawny antelope. After low-key discussion, during which people display

> indifference or even negativity at the news of a kill, the meat is fetched for distribution.(Wiessner 1996, p. 178-9)

4.2 Sharing restricted to friends in large groups

There are no studies investigating the effect of relationship quality on food sharing patterns. Several studies have tested the effect of geographical proximity on sharing behavior, however. Based on the tolerated theft model it is argued that it is impossible to conceal an acquired food from a neighbouring household. As a consequence, sharing frequency between geographically close households is expected to be higher than sharing frequency between distant households (Bird and Bird 1997; Gurven et al. 2000b; 2001). An alternative explanation might be that geographical proximity is associated with relationship quality. Thus, families with a good relationship might be motivated to settle in close proximity (Gurven et al.2000b, p. 210). The results show indeed a higher frequency of sharing between geographically close households. Considering that all relevant studies concern relatively large groups (23, 37 and 84 households for the Ache, Hiwi and Meriam respectively), these results are also supportive to the hypothesis that in large groups sharing is restricted to a limited number of "friends".

Moreover, the idea that individuals restrict their sharing practices to a limited number of group members is in agreement with the observation that the number of households that receive shares from a distribution (sharing breadth) is generally low, as was reported for the Hiwi, Ache and Yanomamö (Gurven et al. 2000b, p. 188; Gurven et al. 2001, p. 282; Hames 2000, p. 402). However, based on these three studies one should not conclude that low sharing breadth is characteristic for *large* groups. Although both the Hiwi and Ache groups are relatively large (37 and 23 nuclear families, respectively), Hames (2000) found similar results for four Yanomamö villages (Venezuela) ranging from six to sixteen households.

4.3 The importance of need

In the cultural anthropological literature, many references can be found to "an ethos of generosity" and "a web of mutual obligation," leading in a natural way to an optimal food distribution for the band as a whole (Balicki 1986; Bird-David 1990; 1992; Endicott 1988; Hiatt 1982; Kelly 1997; Wiessner 1996). An example is given by Marshall (1976):

> The !Kung custom of sharing meat helps to keep stress and hostility over food at a low intensity. The practical value of using up the meat when it is fresh is obvious to all, and the !Kung are fully aware of the enormous social value of the sharing custom. The fear of hunger is mitigated: the person with whom one shares will share in turn when he gets meat; people are sustained by a web of mutual obligation. If there is hunger; it is commonly shared. There are no distinct haves and have-nots. One is not alone. (Marshall 1976, p.295)

The importance of need is also expressed by *the absence of a clear obligation to repay*. Returns are not stipulated by quantity, quality or time, and counter-obligations are overtly denied. Instead, one who has gives to one who needs (Wiessner 1982 p.67). According to Harris (1980 p. 226-227):

> In reciprocal exchanges the flow of labor products and services is not contingent upon any definite counterflow. The partners in the exchange take according to need and give back according to no set rules of time or quantity. (Harris 1980 p. 226-227)

Quantitative studies generally operationalize need as family size. Most studies investigating the effect of family size are inspired by the tolerated theft model. The reasoning is that, compared to smaller families, larger families have more power of persuasion when extracting shares from the acquirer of a food resource. The same prediction was made by Aspelin (1979), however, who aimed to provide a quantitative test of the ethos of generosity in his sharing study on the Mamaînde. Results from the Mamaînde, the Meriam, and the Hiwi show that larger households receive larger shares of food (Aspelin 1979; Bliege Bird and Bird 1997; Gurven et al. 2000b). However, when applying a measure of family need that controlled for the number of producers in a family to Yanomamö sharing data, Hames (2000) found no positive correlation between family need and the amount of food received, thus contradicting the importance of need.

5 Empirical tests of scorekeeping

Based on the reciprocal altruism model, evolutionary anthropologists predict that an individual's act of giving food to another individual is contingent upon the benefits received from this individual. Furthermore, individuals should avoid to give food to potential free-riders. Conversely, individuals should also avoid to give the appearance of being a free-rider. The combination of the kin selection model and the reciprocal altruism model leads to a prediction about a difference in sharing behavior towards kin versus non-kin. Related individuals share part of their genes, so the benefits of free-riding are low. As a consequence, related individuals should be less preoccupied with scorekeeping than non-related individuals. A final hypothesis concerns the possibility that by taking only food transfers into account, the degree of balance will be underestimated. Part of the balance might be in intangibles. Thus, hunters might trade food for sexual favors by female group members. This leads to the following hypotheses:

1) Giving is contingent upon receiving.
2) Contingency is stronger for non-kin than for kin.
3) Individuals avoid to give to free-riders.
4) Individuals avoid to be considered like a free-rider.
5) Hunters trade food for sex.

5.1 Giving is contingent upon receiving

Most attention has been paid to the first hypothesis. Although a strict test of contingency between giving and receiving requires a temporal analysis of sequences of behavior, most studies are limited to correlational measures. Some studies only report correlations on the *generalized level*, that is, the correlation between shares received from all other households and shares provided to all other households (e.g., Hawkes et al. 2001), whereas other studies report correlations on the *dyadic level*, that is, the correlation between the shares household A received from household B, and the shares household A provided to household B (e.g., Hames 2000).

Hawkes and coworkers (2001) and Bliege Bird and coworkers (2002) did not find significant correlations on the generalized level among the Hadza (Tanzania) and Meriam (Melanesian Islands), respectively. On the other hand, the majority of the studies testing for correlations on a dyadic level did find a

significant positive correlation between the amount of food given and the amount of food received. In contrast to most studies testing different evolutionary anthropological models, Hames (2000) explicitly confronted Sahlins' concept of generalized reciprocity (Sahlins 1972) with the evolutionary anthropological model of reciprocal altruism. For all four Yanomamö villages under study he found positive correlations between the number of times food was given and the number of times food was received, on a dyadic level. Furthermore, although he did find, similar to Aspelin (1979), positive correlations between the number of consumers within a family (family size) and the frequency of receiving food, the correlation disappeared when he used a more accurate measure for family need, namely the number of consumers, controlled for the number of producers. Based on those results, Hames concluded that sharing among Yanomamö is balanced rather than generalized (Hames 2000, p. 411). In addition, studies among the Hiwi and the Ache, conducted by Gurven and coworkers (2000b, 2001) yielded significant correlations between the relative amount of food given by A to B and the relative amount of food given by B to A. More importantly, they also conducted multivariate regression analyses and found the relative amount of food given by B to A to have the strongest effect on the relative amount of food given by A to B, even when including such variables as family size, geographical distance, and relatedness (Gurven et al. 2000b, 2001).

One explanation for the different results between studies employing correlations on the generalized level and studies employing correlations on the dyadic level might be a methodological one: the number of cases used to calculate correlations on the dyadic level is larger than the number of cases used to calculate correlations on the generalized level. Thus, correlations on the generalized level might be non-significant simply because the number of cases is too small.[9] In contradiction to this explanation, Bliege Bird and coworkers, calculating correlations both on the generalized and on the dyadic level, found no significant result on either level (Bliege Bird et al. p. 311-313).

A second explanation concerns a difference in the use of absolute versus relative measures of share size. The absence of balanced exchange on the generalized level, as found by Hawkes and coworkers (2001) and Bliege Bird and coworkers (2002), was based on correlations between *absolute* share sizes, that is, on amounts measured in kilograms or calories. In contrast, both studies by Gurven and coworkers (2000b, 2001), reporting significant correlations between shares received and shares provided, use relative measures of share size. More specific,

[9] This was pointed out to me by Michael Gurven (personal communication).

Gurven and his coworkers (2000b, 2001) based their results on *the percentage of the giving household's total production* (in kilograms) that was given away. As a consequence, two households with highly different amounts of food given to each other may be labeled as being engaged in a balanced relationship. If household A gives 10 units of its total production of 100 units to B, and B gives only one unit of its total production of 10 to A, they both give away 10% of their total production. It is doubtful whether such a result should be interpreted as scorekeeping. If A makes his shares to B contingent upon B's relative shares to him, he takes into account B's *ability to give*, or the amount of food that B *is able to miss*. By using a relative measure of share size, the empirical difference between a scorekeeping mechanism and a bonding mechanism becomes very small. (See Section 6 for an elaboration of this argument.) A similar argument can be made with regard to Hames' (2000) study, where conclusions about balanced exchange were based on *frequencies* of exchange. The only study testing for balanced exchange using absolute measures of share size (i.e., number of calories), is the study by Bliege Bird and colleagues (2002). As was mentioned before, this study did not provide support to giving being contingent upon receiving.

5.2 Contingency stronger for non-kin than for kin

Two studies have explicitly tested the hypotheses that non-related individuals are more concerned with keeping scores than related individuals. First, Pryor and Graburn (1980) tested Sahlins' prediction about the degree of balance in relationships with kin versus relationships with non-kin among Sallamiut Eskimos. Two types of benefits were considered: gifts and hosted visits (in which the visitors were generally offered food). For both gift giving and visiting, weighted and standardized net account indices were calculated. Next, standard deviations were compared of those who engaged in gift giving and visiting primarily with near kin, those who engaged in gift giving and visiting primarily with distant kin, and those who engaged in gift giving and visiting primarily with non-kin. The differences in standard deviations between non-kin, distant kin and near kin were non-systematic and non-significant. Based on these results, Pryor and Graburn rejected the hypothesis that net accounts of visits and gift giving are more balanced with decreasing genealogical distance.

Second, Gurven and his coworkers (2001, p.286) used a different measure to compare the degree of balance in benefits received and provided for non-related and closely related families. They found that, over the entire sample period, the ratio of the relative amount of food given by nuclear family A to nuclear family B,

and the relative amount given by B to A, was significantly higher for closely related nuclear families than for distantly and unrelated nuclear families (0.45 and 0.22 respectively). Based on this result, Gurven and his colleagues (2001, p. 286) concluded that *"much of what was assumed to be kin-selected behavior in humans may actually be reciprocal altruism",* but it seems highly unlikely that individuals would be more concerned about being cheated (and thus, engage in scorekeeping reciprocity) in interactions with kin than in interactions with non-kin. Therefore, it seems plausible that correlations, even if controlled for other variables, do not provide a good operationalization for giving being contingent upon receiving. To determine whether A's giving to B is contingent upon B's giving to A, sequential analyses of sharing interactions should be performed (See Section 6).

5.3 Avoidance of giving to free-riders

Hawkes and coworkers (2001, p.126-8) reasoned that hunters who are unsuccessful in capturing prey will not be able to repay their debts and will therefore be excluded or otherwise punished. The results, however, showed that Hadza hunters with lower acquisition rates received no less meat than did hunters with higher acquisition rates. Hawkes and coworkers also tested whether hunters who spend less time hunting receive less food, compared to hunters who spend more time hunting. This hypothesis was also not confirmed. In another study, the question was addressed whether consistently high food producers receive more food when they are indisposed than do consistently low food producers (Gurven et al. 2000a). The results showed no difference between the amount of food given to more successful and less successful food producers in case of sickness or injury.

The argument could be made that unsuccessful foragers are not necessarily free-riders. It is possible that group members do not evaluate the absolute amount of food someone gives away, but the amount of food controlled for this person's total production. In this way, stingy hunters, who acquire considerable amounts of food but keep most of it to themselves, are distinguished from unsuccessful hunters, who simply have little food to give away. Like in the case of the relation between relative amounts of food provided and received (see Section 5.1), taking into account a hunter's total food production, that is, his ability to give, implies at least a minimal degree of generosity. Therefore, it is doubtful whether support for this hypothesis should be interpreted as strong support for scorekeeping. Be that as it may, the empirical results are inconclusive. Bliege Bird and her colleagues (2002, p. 313) found that successful hunters who share relatively little, do not receive less than do successful hunters who share relatively much. In contrast, Gurven and his

coworkers (2000a, p. 270-271) found that individuals sharing a larger proportion of the food they produced, receive more food when they are indisposed than do persons who share proportionately less.

5.4 Avoidance of being considered a free-rider

If sharing behavior depends on one's outstanding debts, unsuccessful hunters, who acquire relatively little food in each hour they hunt, might try to compensate by spending more hours hunting and giving away larger proportions of their prey (Hawkes et al. 2001). Contrary to their expectations, Hawkes and co-workers found a positive correlation between hunting success among the Hadza hunter-gatherers and hours spent hunting (p. 128).[10] However, the same study provides some support for the prediction that unsuccessful hunters may attempt to pay off outstanding debts by giving away a larger fraction of their own kills – although this result was significant only for very large prey. Also Kaplan and Hill (1985a, p. 234) rejected the hypothesis that unsuccessful hunters hunt more hours. They found that successful hunters hunt for significantly *more* hours, compared to unsuccessful hunters, although they do *not* keep more food for themselves and their families.

5.5 Hunters trade food for sex

The trade model was introduced by Kaplan and Hill (1985a, 1985b; Hill and Kaplan 1993), as an answer to the question of why successful hunters hunt more hours and provide more food to others than do unsuccessful hunters. In the case of trade, successful hunters give food to others and receive other benefits in return from those others. As examples of fitness benefits, a lower probability of infanticide on one's offspring, remaining longer at the same location in case of illness, and increased reproductive success are mentioned (Kaplan and Hill 1985a, p. 237).

Empirical tests of the trade model have been restricted to the exchange of food for sex. Thus, Kaplan and Hill (1985b) compared the number of surviving

[10] To exclude the possibility that the positive correlation between hours spent hunting and acquisition rate was the result of just being two sides of the same coin, Hawkes and co-workers (2001 p. 128-129) attempted to distinguish between skill and effort. They found that seasonal acquisition was positively correlated with the overall rate of food acquisition, controlling for overall hours spent hunting. No such correlation was found, however, between hours spent hunting and seasonal acquisition, controlling for the overall rate of acquisition. From this they concluded that skill (overall acquisition rate) was a better predictor of hunting success than was foraging effort (hours spent hunting).

children, illegitimate children and extramarital affairs of successful and unsuccessful hunters. For all three variables they found that successful hunters score significantly better than unsuccessful hunters.

However, since the trade model explicitly states that successful hunters are rewarded by *the persons who have received meat*, rather than by their *group members in general,* as was predicted by the models of indirect reciprocity (Hawkes 1993b), Kaplan and Hills' (1985b) study does not constitute an adequate test of the trade model. It does not address the question of whether the reproductive benefits are provided by the persons to whom the hunters gave the meat, so what is actually tested is the indirect reciprocity model. As was argued before (see Section 3.2.4), sharing patterns that are the result of indirect reciprocity are not relevant to the question that is dealt with in this paper, since the absence of a return benefit by the recipient cannot be interpreted as an indication of free-riding.

6 Discussion

6.1 Summary

Although there are no studies explicitly testing the idea that sharing patterns are the result of a mechanism for helping those group members or friends who are in need, regardless of possible imbalances, the available evidence is generally favorable to a bonding interpretation of sharing behavior. Thus, both qualitative accounts of the role of the hunter, and quantitative studies testing for equal sharing, provide support to egalitarian sharing patterns in small groups. The hypothesis that in larger groups, sharing is restricted to clusters of friends, could only be tested in an indirect way. Several studies provided support to the idea that sharing is clustered and that geographical proximity is a determinant of sharing behavior. However, these patterns were not only found in large groups, but also in some small groups. Finally, the importance of need was supported by cultural anthropological accounts stressing generosity and mutual obligation. In addition, evolutionary anthropological studies, operationalizing need by family size, found a positive effect of need on the amount of food received. In contrast to these results, however, Hames (2000) demonstrated that the effect of family size disappeared when controlling for the number of producers in a family.

The results of the evolutionary anthropological studies do not provide much support to a strict scorekeeping mechanism in the sense of keeping scores of absolute amounts provided and received. Studies focusing on correlations between absolute amounts of food provided and received, fail to report significant results.

Furthermore, there is no support that individuals avoid to provide benefits to persons who might not be able to pay off their debts: hunters with low acquisition rates receive as much as hunters with high acquisition rates. Neither was there evidence that poor hunters seek to improve their credit by hunting more hours. Finally, although it is possible that hunters may exchange food for benefits in a different currency, for example sex, this has not been properly tested.

A frequently expressed reaction to these results is that the time frame considered is too short to reveal a pattern of balanced exchange. It is claimed that, in the long run, benefits provided and benefits received might be approximately balanced (Altman 1993, p. 352; Bliege Bird et al. 2002, p.315; Hames 2000, p. 411; Kaplan and Hill 1985a, p. 234). If that is the case, however, it seems unlikely that sharing behavior is the result of a scorekeeping mechanism. First, lengthy delays make it difficult for foragers to keep account of their debtors. Second, such delays raise discounting problems: benefits returned to me now yield higher fitness benefits than do benefits returned to me next year (Bliege Bird et al. 2002, p. 316; Gurven et al. 2000b, p. 180; Hawkes 1992).

Nevertheless, there are some studies suggesting that giving is contingent upon receiving. These studies apply relative measures of share size, that is, the amount of food that is given away as a percentage of one's total production. Thus, several studies have reported significant positive correlations between the relative amount given and the relative amount received, or between frequencies of sharing instances. In addition, although there was no evidence that giving to unsuccessful hunters is avoided, there was some evidence that people avoid to give to stingy hunters, who are successful but who share only a small percentage of their kills. These results are in line with the idea that hunter-gatherer food sharing patterns are guided by a mild scorekeeping mechanism: in order to avoid exploitation by free-riders they give to those who give to them, but they do not match their shares to the exact amounts they have received. Opposing this idea, however, was the finding that correlations between the relative amount given and the relative amount received were higher for interactions between kin than for interactions between non-kin.

In sum, the findings from studies on hunter-gatherer food sharing do not provide unambiguous support to one of either proximate mechanisms. Both the bonding and the scorekeeping mechanism receive some support. In the following two sections, however, I argue that the available evidence for balanced reciprocity or scorekeeping mechanisms is not adequate. Two points are made: *1) relative measures confound with need*, and *2) to demonstrate a scorekeeping mechanism one needs to perform sequential analyses*.

6.2 Relative measures confound with need

The use of relative measures of share size has been inspired by the incorporation of bargaining economics in models of food sharing (Boyd 1992; Gurven et al. 2000b; Hill and Kaplan 1993; Sosis et al. 1997). If an individual gives away only small amounts of food, it might still be advantageous for a successful hunter to provide him with frequent shares – provided that the benefits of receiving those occasional small shares minus the costs of giving away the larger shares are greater than the benefits of a situation in which no "bargain" occurs. Therefore, even unbalanced exchange – in terms of absolute quantities of food – can be in accordance with the assumption of fitness maximization. It seems, however, that if hunters are guided by bargaining considerations, even though they may prefer a *relatively unfavorable exchange* to *no exchange*, they will still prefer a *relatively favorable exchange* to *a relatively unfavorable exchange*. Thus, one would still expect good hunters to share mostly with other good hunters, and as a consequence, poorer hunters to share mostly with other poorer hunters. If this would not be the case, the assumptions of bargaining economics would be violated: good hunters would help the weaker ones even in the presence of more favorable bargains to be struck. Note that the last situation is in line with the bonding mechanism: an individual's sharing behavior is guided by the *need* of others, rather than by the avoidance of misbalances.

In sum, a significant correlation between the relative amount of food given by A to B and the relative amount of food given by B to A, can be the result of both a scorekeeping and a bonding mechanism. It would point to a (mild) scorekeeping mechanism if good hunters share primarily with other good hunters, and occasionally strike a relatively unfavorable bargain with a poor hunter. In contrast, it would point to a bonding mechanism if good and poorer hunters shared indiscriminately with each other. To discriminate between the two mechanisms, one should test a model in which, in addition to the relative amount of food given by A to B, also separate variables measuring A's total production and B's total production should be included as explanatory variables. The analyses by Gurven and his coworkers (2000b; 2001) and Hames (2000) did not include these variables. Therefore, the significant effect of the relative amount of food given by B to A on the relative amount of food given by A to B does not unambiguously point to scorekeeping.

6.3 To demonstrate a scorekeeping mechanism one needs to perform sequential analyses

The last point that needs to be made with regard to the alleged evidence for scorekeeping reciprocity is that *even if* the empirical studies had shown a consistent pattern of significant correlations between the amount of food given away and the amount of food received, this would not necessarily imply that sharing is based on a scorekeeping mechanism. The finding that on the long run, *sharing patterns are balanced*, does not mean that *the proximate mechanism for sharing behavior is concerned with maintaining a balance between food received and food provided.* If A and B help each other unconditionally when one of them is in need, and if both have the same chance of getting in need, on the long run the frequencies of helping will be equal, and the correlation between the number of times A has helped B, and the number of times B has helped A, will be 1. Although unconditional sharing seems to contradict the assumption of fitness maximization, the conditions in the ancestral environment might have favored the selection of a bonding mechanism. Since groups were small, consisting of many kin-related individuals, and since food was unpredictably acquired, a proximate mechanism for helping group members who are in need might have had sufficiently low fitness costs and sufficiently high fitness benefits to have evolved.

Since both the scorekeeping mechanism and the bonding mechanism would predict sharing patterns to be balanced on the long run, correlations between the total amount of food received and the total amount of food provided do not suffice. Rather, sequential data about sharing acts are needed. If sharing behavior is the result of a scorekeeping mechanism, A's behavior towards B at time 3 will be dependent on what happened at time 2 (and if one allows for a longer memory span, also on what happened at time 1). In contrast, if sharing is the result of a bonding mechanism and B is in need, A's behavior towards B will be solely dependent on the degree to which A is concerned about B's welfare (see Figure 1). With this distinction in mind, the unexpected result that correlations between benefits given and benefits received was higher for interactions between kin than for interactions between non-kin, loses its mystery. Individuals do not match the shares received from kin more strictly than the shares received from non-kin. Related individuals just share more. Whereas many non-related individuals do not share at all, sharing between related individuals is very frequent, because they are more concerned about each other's welfare.

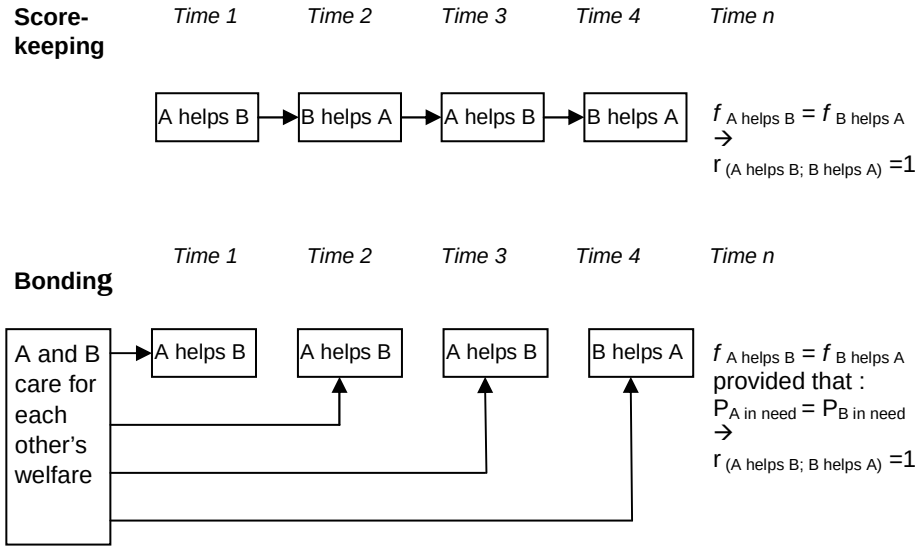

Figure 2.1: Sequential sharing according to the scorekeeping and the bonding mechanism

In sum, based on this review I do not pretend to have demonstrated that sharing behavior is guided by a bonding mechanism. If anything has become clear, it is that sharing patterns *per se* do not give much information about the proximate mechanisms for sharing behavior. To test whether one of either mechanism can account better for sharing behavior, sequential data of food sharing are needed. I do claim, however, that considering the available evidence from anthropological studies on food sharing, the important role ascribed to scorekeeping reciprocity and cheater detection in evolutionary game theory and evolutionary psychology is not justified.

CHAPTER 3

Reciprocal altruism under conditions of partner selection[1]

1 Introduction

This paper is a contribution to solving the problem whether cooperation, in the form of reciprocal altruism, can emerge and maintain itself in a population of selfish individuals. We use an evolutionary game theoretic simulation model [the Social Evolution Model (SEM); De Vos and Zeggelink 1997] for investigating the relative fitness of two versions of a reciprocal altruistic trait competing with a defecting trait. One main difference between The Social Evolution Model and most of the models that are known in this field is that *partner selection* is straightforwardly built in the strategies of the players. In most of the models in the literature, partner selection is not an option in the game (see below for exceptions). Because of this element of forced play, much attention is given to the ability of strategies to detect cheaters and to retaliate (to an appropriate degree). We will show that modeling partner selection points to disadvantages of a preoccupation with cheater detection and to the importance of committing oneself to a partner.

We interpret the SEM as an evolutionary game theoretic model for the study of reciprocal altruism. We concur with Stephens' (1996) impression of a

[1] This chapter has been published (de Vos, H., Smaniotto, R. and Elsas, D.A. (2001). Rationality and Society, 13, 139-183). We thank William Brown, Evelien Zeggelink, and two anonymous reviewers for helpful comments.

widespread agreement that the following four conditions are individually necessary and jointly sufficient for an instance of reciprocal altruism:

1) The behavior must reduce a donor's fitness relative to selfish alternatives;
2) The fitness of a recipient must be elevated relative to non-recipients;
3) The performance of the behavior must not depend on the receipt of an immediate benefit;
4) Conditions (1), (2), and (3) must apply to both individuals engaged.

The best-known game theoretic model that is used for the study of reciprocal altruism is the iterated Prisoner's Dilemma game (iPD). Some modified versions of this model were specially constructed in order to allow for partner selection. We start with a discussion of how the SEM differs from the iPD and these special versions, and then describe the strategies that we investigate and the simulation design. We conclude with a description and a discussion of the results.

2 Evolutionary game theory and the iterated Prisoner's Dilemma

Cooperative behavior has been extensively studied using (evolutionary) game theory. In this section we give a short description of this model.

The most popular building block of evolutionary game theory is the Prisoner's Dilemma game (PD), in which both players have the choice to cooperate (C) or to defect (D). In its original version, players are not able to withdraw (i.e., they don't have an exit option). The game is characterized by its payoff structure, as follows:

		Player 2 C	Player 2 D
Player 1	C	R,R	S,T
	D	T,S	P,P

Both players have the following preference ordering from high to low over the four possible outcomes of the game: T > R > P > S.[2] Because the dominant strategy is defection for both players, the equilibrium outcome is (P,P). This outcome is deficient, because a move to (R,R) would be Pareto-optimal. This move requires the cooperation of both players.

The iterated PD (iPD) is simply a repeated version of this same type of interaction structure. The iPD requires as a second condition: (T + S) < 2R. This is called the *anti-exploitation condition*. It is considered necessary because otherwise alternating exploitation would be more advantageous than mutual cooperation (Axelrod and Hamilton 1981; Maynard Smith 1982). The central problem is whether there is a cooperative evolutionary stable strategy (ESS) for individuals in a population who play iPD's with each other. An ESS is defined as a strategy that cannot be invaded by a mutant strategy, that is, if all individuals in a population adopt the ESS, then no mutant can invade that population under the influence of natural selection.

According to Maynard Smith (1982), one of the founders of evolutionary game theory, an explicit genetic model may be needed when the phenotypic treat of interest is itself concerned with the process of sexual reproduction, so that appropriate fitnesses can only be calculated for a sexual model. But if the phenotype (strategy) considered could have been produced by a genetic homozygote, there is no reason to build genetics into a model meant to explain at the level of the phenotype.[3] The step from game theory in general to evolutionary game theory is set by replacing the notion of rationality with the concept of population dynamics and stability, and by replacing utility (self-interest) with Darwinian fitness.

Axelrod (1984) investigated the strengths and weaknesses of several strategies that players might adopt, using the strategy characteristics nice, retaliatory, and forgiving. A strategy that combines these characteristics seemed to be superior in a population of different kinds of strategies.[4] A strategy called Tit for Tat (TFT), that conforms to these desirable characteristics, consists of the following rule of behavior: I start with presuming my opponent to be cooperative, and thereafter I mirror his choices.

One of the factors that determine the success of TFT as a strategy in the iPD is the extent to which the players value future outcomes less than present

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2 T stands for Temptation, R for Reward, P for Punishment, and S for Sucker's payoff.

3 Maynard Smith (1982) defines an evolutionary stable strategy in its standard form on the basis of the assumption of parthenogenetic inheritance.

4 See Martnez Coll and Hirshleifer (1991) for a critical discussion.

ones (this is expressed in a discount parameter). TFT does very well especially when the shadow of the future heavily shapes present behavior, an alternative way of stating that the discount parameter should be relatively high. This may be extended to the expectation of a series of interactions that will go far enough in the future. To compute the consequences of these assumptions, the compound payoff of the iPD is calculated as the geometric series in which the one-shot game payoff is the first term and the discount parameter is the constant ratio of a payoff to the payoff of the foregoing game.

Axelrod used computer simulations to study the iPD. The computer program made the different strategies play a number of times to each other, each strategy being represented by one player. From these simulations he could observe how well the strategies did when repeatedly playing to each of the others.

3 The Social Evolution Model

The SEM differs from the iPD in the following four main respects. First, nature (or fate) is added as a player. Second, in the SEM, cooperation is always solicited and is a response to an explicit request, which does not exist in the iPD. Third, in the SEM, players are not externally assigned to each other, but the assignment process (partner selection) is part of their strategies. And finally, fitness is modeled in a different way. We give a short explanation for each of these differences.

In the first place, in the SEM, nature is added as a player.[5] The structure of the iteration is a compound game that consists of a series of one-shot games that is iterated. The compound game that is iterated (hereafter called a round) begins with a game that is played by nature with each of the other players. In those games, every player runs the risk of going into distress according to a probability that is set as a model parameter. Thereafter the individuals who are hit by nature (who are distressed) have to look for help from one of the individuals who are not hurt by fate. Those of the distressed players who do not find a helping player do not survive (and are removed from the population). Since the second and the third differences are closely related, we explain them together.

The iPD repeats a number of one-shot games in pairs for each of the strategies introduced in the system. So the ultimate interaction structure from which information is gathered is the (one-shot) PD. In the PD game, when the

[5] In earlier descriptions of the SEM (De Vos and Zeggelink 1994; 1997) nature was not considered to be a player. Because of that the interaction structure as modeled by the SEM was not presented as a game.

two interacting individuals play a single round of the game they act simultaneously (at least both players act before they have seen the choice of their opponent). And the iteration over pairs of strategies implies that the same two individuals interact repeatedly, accumulating evidence concerning the choices made by their opponent in the rounds that were played so far. This makes the iPD an instrument to observe the strengths and weaknesses of the strategies involved.

In the SEM, cooperation means, Grant a request for help, and defection means, Refuse to grant such a request. This makes the SEM an attractive instrument with which to study the emergence and the viability of reciprocal altruism. It represents a self-regulating system. The structure of the interactions is shaped as a pair of consecutive actions. This is realized in a simple way: each interaction is in fact half of an interaction as played in the PD. The first half consists of player A's decision to grant (or refuse) player B's request for help. Helping a distressed player temporarily reduces the fitness of the player who helped. The probability of his getting into distress is larger the very next time that he is engaged in a game against nature. The second half of the interaction consists of player B's decision, at a later moment, to grant (or refuse) player A's request. So we see that help is *delayed* instead of immediately reciprocated. And it is only given, and returned, in response to an explicit request.

So when nature has turned part of the players into a state of distress, each of the players in distress asks for help from one of the other players. A player who is asked for help, has to react with either 'cooperate' (provide help) or 'refuse to help', a response that is either a defection or an expression of not being able to afford help to give. This reaction is in fact the basic action from which the PD interactions are built. So the element that has been built in the SEM that is unknown to the PD is the act of asking for help by the players who got in distress and the act of players who were asked for help to give or refuse (or to select a recipient of help if asked by two or more others). This new element is in fact *partner selection.*

There may be different reasons for a refusal to grant a request for help. The individual asked may have helped already the maximum number of individuals she can help during a round (one in our setting). Or she may be in distress himself or just recovered from that state in the same round, in which cases she is not capable to help others. Or she just defects.

How players approach others for asking help, and how players decide whether to help an individual, is determined by their strategy. Although the interactions that take place in the SEM are asymmetric, in contrast to those that take place in the PD, all players may get in distress in a future round. By assuming

that players are aware of this, reciprocal altruism can really be modeled. A player who provided help to another player, hopes to get help in return when he asks that player in the future.[6]

The delay of cooperation makes the interactions that are modeled by the SEM (and for that matter, the modified iPD; see note 6) more like (than the iPD) what sociologists and anthropologists refer to as: (the norm of) reciprocity as insurance, risk reduction by way of food sharing, social exchange (instead of economic exchange), or simply, *delayed exchange of help* (Blau 1989; Cashdan 1985; Ekeh 1974; Gouldner 1960, Kurland and Beckerman 1985, Sahlins 1972, Wiessner 1982, Winterhalder 1986, Woodburn 1982,). And the fact that players in the SEM have to ask in order to receive help instead of receiving unsolicited help, makes these interactions very similar to the practice of *demand sharing*, which seems to be more prevalent in egalitarian hunter-gatherer societies than unsolicited generosity or gift-giving (Peterson 1993).[7]

The fourth difference between the SEM and the iPD concerns the treatment of the notion of fitness. In the iPD simulations, the fitness of a strategy is modeled as a function of its accumulated payoffs. In the SEM, the fitness of a strategy is the proportion of the number of surviving players enacting that strategy relative to the total number of surviving players at the end of a simulation. If this proportion is higher or lower than it was in the beginning population, its fitness is higher or lower than the one of the competing strategy (if there is only one).

Although the SEM is clearly more realistic than the iPD, it has its limitations (see also the last section of this paper) and restrictions. Several restrictions have been added as changeable values of parameters. An individual who has already helped one other player cannot deliver help to a second player during the same round. This parameter leaves open possible future research in which a player is able to help a number of individuals, reducing her own fitness

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6 That cooperation is delayed instead of immediately reciprocated, makes the SEM, in a formal way, similar to the *modified PD*, one of the games, different from the (standard) PD, that according to Stephens (1996) also fulfills the informal conditions for reciprocal altruism (see above). The modified PD is simply a PD minus the anti-exploitation condition. Stephens argues that an iPD minus this condition (or more precisely: with $(T + S) \geq 2W$)) also fulfills these informal conditions, because alternating 'exploitation' can easily be considered as a form of cooperation, the benefits being mutual. Each player allows itself to being 'exploited' (in SEM terms: is prepared to help) at a certain moment in exchange for the opportunity to 'exploit' the other player (in SEM terms: in exchange for return of help) at a future moment. Cooperation is not immediately reciprocated, but is delayed. In fact, if we add nature, as a player who generates probabilities of distress, and if we introduce asking behavior of the distressed players, and granting and refusing behavior of the players that are asked, than we turn the modified iPD into the SEM!

7 Recently, Neilson (1999) constructed a formal iPD model of favor exchange. The process of favor exchange appears to be identical to demand sharing.

further with each additional individual helped. Players whose request for help is not granted have two other opportunities to ask for help. So the round consists of three subperiods in each of which the players (still) in distress ask for help. The number of sub-periods is also a parameter setting that might be changed in future research.

In Section 4 we compare the SEM with versions of iPD models that involve some kind of partner selection.

4 Versions of iPD models involving partner selection

Simulations with the iPD showed that invasion by cooperators is possible only if TFT strategists meet each other with some minimum threshold frequency, so that they can reap enough benefits of cooperation (Boorman and Levitt 1980, Boyd and Richerson 1985, 1988, Reeve 1998). This *initial clustering of the population*, in which reciprocators meet each other more often than they meet defectors, simply is assumed to take place, by way of some process external to the process of cooperation itself.

As far as we know, it has not often been considered that this unsatisfactory state of affairs may be an *artifact* of using the iPD as the paradigmatic social situation for studying the viability of a reciprocal altruistic type of cooperation. In general, in iPD models players are forced to play with each other. As said, every player is sequentially assigned to all other players, to a random set of them, to a random set of the same subgroup to which each individual is externally assigned (Dugatkin and Wilson 1991) or to their neighbors to which they are, again, externally assigned (e.g., Nowak and May 1992, 1993). This means that the potentials of *partner selection* by the players themselves are ignored. Our, and others', intuitive understanding of how reciprocity could evolve suggests that the ability to select partners might be an important condition for a successful invasion process.[8]

Others (Dugatkin and Wilson 1991; Tullock 1985; Kollock 1994; Yamagishi et al. 1994) have noted these restrictions of the iPD. We know of several attempts to include partner selection in iPD game-theoretic simulations.

First, actors were given an exit-option or a refuse-option, a third alternative besides cooperate and defect (Dugatkin and Wilson 1991; Hayashi

[8] Sober and Wilson share this intuition: 'The idea that choosing associates favors the evolution of altruism is deeply intuitive, but it has received little attention from evolutionary biologists' (1998, p. 135).

1993; Macy and Skvoretz 1998; Nettle and Dunbar 1997; Schuessler 1989; Vanberg and Congleton 1992; Yamagishi et al. 1994).[9] In these ways a wider range of behavior is modeled. But although actors can leave a partner or refuse to interact with someone, they cannot decide which others to approach.[10]

Second, simulations in which approach behavior is also included were reported by Yamagishi et al. (1994) and Watanabe and Yamagishi (1999). Yamagishi et al. (1994) designed selection strategies for selection of partners for each trial in which a two-person PD was played. Each selection strategy was combined with one of a number of action strategies, that is, a strategy for playing the game. A game was played only if two actors selected each other. A weakness of this way of modeling is that the two strategies are theoretically unconnected: every selection strategy is combined with every action strategy. Watanabe and Yamagishi (1999) modeled partner selection by increasing the probability of selecting a partner as a consequence of the partner's behavior in the preceding PD that was played with this partner. In this way a clustering of TFT-players emerged. Also in this procedure selection is simply added to the PD strategy.

Third, Cooper and Wallace (1998) let players choose between whether to match randomly or form fixed partnerships. To do this, they had to distinguish a matching phase and a playing phase. Similarly, Stanley et al. (1995) had to distinguish a phase in which offers of game play are made. So, in these models partner selection is not a part of the playing strategies, as it is in the SEM.

Fourth, Wilson and Dugatkin (1997) start with a population consisting of groups and let players choose the group to which they will be assigned. In the SEM, the population is unstructured to start with, and group formation can be considered a collective outcome of the interactions instead of as initially given.

Finally, Flache and Hegselmann (1999) modeled partner selection using a cellular automata framework. Each player has an initial position in a two-dimensional cellular grid, has a certain degree of neediness, and plays support games simultaneously with all his neighbors. In every period each player receives a migration option with an exogenous probability. The model makes strong assumptions as to the information each player has: he knows constantly and perfectly all players' positions, their payoffs and utilities of the support game, and their neediness levels.

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[9] A formal model that gives players the option to refuse to interact, on the basis of markers, is Frank (1988). A similar model was developed by Peck (1993), who includes behavior pertaining to the choice of maintaining or leaving a relationship within the strategies, but then randomly assigns players to new interaction partners. See for a tournament approach: Yamagishi et al. 1994.

[10] Experimental studies within the Prisoner's Dilemma game paradigm with choice of exchange partners include: Kollock (1993) and Yamagishi et al. 1998.

In Section 5, we give a more formalized description of the SEM, with a description of the strategies that were investigated by De Vos and Zeggelink (1997), and the strategies we investigate in this paper.

5 The structure of the SEM

At the start of a simulation run a generation of actors is generated. A generation consists of one or both of two kinds of players: a cooperative (reciprocal altruistic) phenotype and a defecting phenotype. The proportion of cooperators at the start of the simulation, S_i of the N_i players in total, is varied over the various runs of the simulation (please note: index i stands for 'initial' and not for a subscript running over a range). To allow comparison, we use the same parameter settings used by De Vos and Zeggelink:

N_i = 10, 20 (and as added new value:) 50
S_i = 0.0, 0.1, 0.2, …, 1.0 with N_i = 10,
S_i = 0.0, 0.05, 0.10, …, 1.0 with N_i = 20, and
S_i = 0.0, 0.02, 0.04, …, 1.0 with N_i = 50.

This means that simulation runs are repeated for 0, 1, 2, ..., to N_i cooperators among a total of N_i players.

After the generation of players in one generation, the compound game, consisting of a first move by nature (bringing distress to some players) followed by three subperiods of help-seeking (see below), is repeated 30 times (rounds). Then the fraction of cooperators still alive (S_e) among the total of players still alive (N_e) is taken as indicating the fitness of the cooperative phenotype (provided that N_e>0). This fitness is computed for 50 repetitions of the same simulation run (parameter setting). The mean fitness is taken as an unbiased estimate of the 'real value'.

To iterate the compound game, some additional parameter values must be set. Here again, the choices are made in accordance with the values used by De Vos and Zeggelink. The probability used by nature to distress players is set to q = 0.2, 0.1, 0.05.

The costs of helping are expressed as proportions of the probability of getting in need after helping another. So in the next round after helping the values of c are c = 1.5q, 1.25q, 1.125q.

It seems realistic that the costs of helping are linearly related to the probability of becoming distressed: in bad times it is riskier to give up resources than in good times. We only consider acts of helping that involve costs, that is, reciprocal altruism in Trivers' (1971) sense.[11]

It is clear that the highest of the probabilities to become distressed represents extremely adverse conditions. As has been pointed out above, this should be interpreted as the environmental conditions in which the chances are highest that reciprocal altruism is of some importance. If it is not in these conditions that it contributes to the altruist's survival, than we should seriously doubt whether it could exist at all. But, nevertheless, even in these conditions, if benefits of reciprocal altruism fall upon the reciprocal altruists, it is still possible that the defectors reap still higher benefits.

De Vos and Zeggelink investigated two strategies, a cooperative one (prepared to help) and a defective one (asking for help but never helping). The immediate purpose of our simulations is to compare the fitness of the cooperative strategy investigated by De Vos and Zeggelink with that of an alternative cooperative strategy, both in competition with a defective strategy. In later research we hope to investigate alternative strategies to the ones already studied, the effects of changed parameter settings, and the impact of model extensions.

Since we purposely omit kinship relations, our simulations describe a world in which all cooperation is between unrelated individuals. So at the beginning of a simulation the population consists of individuals who are socially isolated, but have an interest in others who can be approached as potential providers of help. The omission of kinship relations makes the problem more easy to handle. It also justifies the choice of some parameter settings that produce low chances of survival. In real circumstances, with cooperation between kin, these chances would be higher, but this would be the case for defectors as well as cooperators.

Our first goal is to compare the cooperative strategy as defined by De Vos and Zeggelink with the newly defined one in this paper. As has been said, this consideration leads us to keep to the parameter settings as used earlier. As a first step to a wider choice of the parameter values, we added a simulation series with $N_i = 50$.

The measure of success of a strategy has two components. First, a successful strategy should be able to resist invasions by other strategies. This is

[11] Another mechanism of cooperation between unrelated individuals, by-product mutualism (Dugatkin and Mesterton-Gibbons 1996), could be examined by keeping costs at zero.

the ability to prevent an increase of players enacting another strategy if they enter one at a time (meaning that the strategy is an ESS), or, as a weaker version, the ability to prevent a complete takeover resulting in a mixed equilibrium. Second, a successful strategy that enters one at a time should be able to invade a population of players enacting another strategy resulting in a complete takeover (strong version), or in a mixed equilibrium (the weaker version).

6 Strategies in the SEM

Since the behavior corresponding with helping or refusing to help is similar to the behavior corresponding with cooperation and defection in a PD game, an appropriate way of modeling a cooperative strategy seems to be taking the TFT strategy as an example. This has some serious complications, however. Corresponding with 'cooperate on the first move' of TFT, in the SEM a social player, A, would be prepared to help another player, B, who asks for help for the first time. But then, under what condition will A help B the second time? Should she require that B has returned help before helping again? But perhaps B did not have the opportunity to provide help, because A did not need help, or A turned to C for help. Not having received help from B does not imply that B defected. Even if A had asked for help and B had refused, it is not certain that B defected, because perhaps B was willing to help, but was in need himself. Or he just ran out of resources because of providing help to D. A real defection would be a refusal to help without any 'excuse,' that is, a defection that was not necessary given the restrictions of the model, but that was generated by the strategy of the player who was asked for help. But A's being able to discriminate between a refusal that is not a defection and a refusal that is requires that B should be enabled to truthfully communicate his intentions. This is a strong requirement that would seriously weaken the relevance of the results.

Besides this, the other half of a cooperative strategy, the principles for selecting others to ask for help, pertains to a completely new kind of behavior relative to the iPD. Therefore the TFT-strategy is after all a rather poor heuristic for devising a cooperative strategy in the SEM.

Similar to the defecting strategy in Peck's (1993) formal model, the defecting strategy in the SEM simply can be chosen as, Ask another individual for help in case of need, if possible avoid asking the same person twice, and always refuse to provide help if asked.

7 Two cooperative and one defecting strategies

In this paper we examine the success of one particular cooperative strategy, called Commitment, in competition with the defecting strategy (Defection). In addition, we compare it with the success of the cooperative strategy examined by De Vos and Zeggelink, to which we refer as Keeping Books Balanced.

We start with a description of the Keeping Books Balanced strategy and of the results of De Vos and Zeggelink.

7.1 Keeping Books Balanced

De Vos and Zeggelink ran simulations with a cooperative strategy that attempts 'to keep the books balanced'. According to this strategy, a player *who is asked for help* (and who is not in need herself) by one other player, refuses to help if the other one is in her debt, and otherwise helps. If two or more who are not in her debt ask her, she chooses the one to whom she is most in debt. If this applies to two or more others, she selects the one to whom she has given help most often; if then still two or more others are left, she chooses randomly. A player *who is in need* randomly asks another player for help, except in case one or more others are in his debt. If there is one, he selects that one. If there are two or more, he chooses the one who has helped him most often or chooses randomly between the two or more who did.

Our reasons for labeling this strategy Keeping Books Balanced become clear if you realize that it has the following two characteristics. First, the strategy is designed in such a way that a cooperative player, A, who has successfully exchanged help with B, and has provided (still) unreturned help to C, turns to C for help instead of to B, who has proven to be cooperative. And second, cooperative players help each other only under the condition that they take turns. More precisely: they strictly avoid a situation in which the number of times they provide help to another player exceeds by more than one the number of times they receive help from that same player. This makes them of course vulnerable to the freak of fate. The course of natural events is not so regular that A and B neatly alternate periods of distress. Both characteristics can be seen as consequences of a wish to keep the books balanced. Once help is given, Keeping Books Balanced insists on receiving help in return, by asking the receiver again and again, and by always refusing to help unless help is returned in between, that is, even if the receiver provided help before.

De Vos and Zeggelink showed that the success of Keeping Books Balanced was restricted to harsh conditions (that is, with high probabilities of being in need) and small populations. In one set of these harsh conditions - if it starts with three or four in a population of 10 (only populations of 10 and 20 were examined) - it was able to take over a population. Under the same harsh conditions in a population of 20, a number of 6 or 7 was enough to produce a population that oscillated around a proportion of 0.5. In all conditions Keeping Books Balanced was able to resist invasion by Defection.

These results can be compared with the pattern of findings from simulations using the iPD. We first see that both the cooperative strategy in the SEM and TFT in the iPD are able to resist invasion by defectors. But in the second place, regarding the ability to invade a population of defectors, TFT needs to be clustered before the process starts, in order to reap the benefits of mutual cooperation. Instead, Keeping Books Balanced needs to enter with a minimum number (in a relatively small population) in order to allow itself to cluster and reap the benefits. In the iPD the clustering, the process of partner selection, is assumed to have taken place before the simulation begins; the clustering process is not an object of study. In the SEM the clustering depends on the nature of the cooperative strategy and is a main object of study.

The ability of Keeping Books Balanced to cluster itself is a consequence of it being steered, *to some extent*, by a commitment principle: in those cases when a selection has to be made, the player prefers the one who has most often received or given help. Therefore De Vos and Zeggelink labeled it reciprocal altruism with a prefer-old-helping-partners-trait. Because of the two characteristics mentioned above, we think Keeping Books Balanced is a more appropriate name. We see that its success is severely limited in terms of the ability to invade a population of defectors: it only succeeds in harsh conditions and in a small population, and it has to enter with considerable proportions (0.3 or 0.4).

Therefore we decided to examine the success of a strategy that gives more weight to the commitment principle and is less concerned about keeping books balanced. Intuitively, one could expect that less insistence on keeping books balanced has a detrimental effect, because of the increased vulnerability to exploitation. But this may be outweighed by the positive effect of the increased weight of commitment, which is expected to facilitate the clustering process. The way in which we model the commitment strategy is explained in the next section.

7.2 Commitment

We describe the helping and asking behaviors of Commitment separately.

Helping behavior

If a Commitment player is asked for help, and is not in need himself and has not already helped someone in the same round (in which cases he refuses to help), he first considers whether he has ever received help from the players who ask him. He provides help if there is only one from whom he ever received help. This shows a high commitment to the player who helped: after a player helps him once, he is willing to help this player repeatedly, without constantly requiring to be reimbursed before helping again. If he is asked by two or more players who have helped him before, he selects that player (if there is only one), from whom he has received help most often. If there are two or more, he selects the one to which he is most in debt (here enters a wish to keep the books balanced); if this applies to two or more players, he randomly selects one of them.

If he is asked for help by two or more from whom he has not received help in the past, he provides help to the one, if there is only one, to whom he did not provide help in the past. If there is no such player who asked - that is, if he is asked by one or more players who have not yet returned received help - he refuses to help (a keeping the books balanced consideration). If there are two or more to whom he has not provided help in the past, he randomly chooses one of them.

So, with regard to helping, the commitment principle emerges in two ways. In the first place, Commitment is prepared to help unconditionally another player who has previously provided help, if she is the only one who asks. And second, if he has to select a receiver of his help from several candidates from whom he has received help in the past, he then selects the one who provided help most often, irrespective of the number of times he returned this help - that is, regardless of the size of his debt.

Asking behavior

If Commitment gets in need, he first considers whether he helped others in the past. If there is one such other player, he asks that one. So, as long as he does not need to select one player from several candidates, he acts in a way that keeps the books balanced. But if there are two or more whom he helped in the past, he selects the one from whom he received help or from whom he received help most often. This consideration is commitment-oriented. Still, it may happen that there are two or more from whom he received help most often. Then he asks the one

that is most in his debt, orienting himself towards balanced books, or, if this applies to two or more, he randomly chooses the one to ask.

If in the past he has helped no one, he examines whether there are others who have not yet helped him in the past. If there is one such player, he asks that one, and if there are two or more, he randomly selects one of them.

If in the past he has received help from all the other players (without him having returned help), he randomly selects one from this set (which is, alas, in vain; see the description of helping behavior above).

It is typical for Commitment to return to others with whom in the past successful exchanges were accomplished.

7.3 Defection

We model defection with the same strategy as in De Vos and Zeggelink: if in need, randomly select another individual to ask for help from those others whom you have not already approached, and if approached, refuse to give. This strategy captures the idea of defection in a straightforward manner: it profits from the presence of a cooperative strategy without bearing the expenses of helping others. Also, defectors realize that they have nothing to gain from asking help twice from the same individual, just as in the ALL D-strategy in Peck's (1993) formal model.

8 Communicational and informational aspects

What do the SEM, in the way we use it, and the strategies that we examine, assume about communicational and information-processing abilities and about information as a resource? Players are able to memorize all their interactions and interaction partners. At the onset of a generation they are informed about the presence of others, and if they get into distress, they know that getting help is the only way to survive. Furthermore, at the beginning of every round they are informed about which other players are still alive.

The transfer of valuable information about the natural environment (for example, about where to find food or shelter) can be considered one possible form of helping. It involves costs if, as a consequence of the transfer, the provider of the information has to share these resources with the receiver. So, this kind of communication 'is allowed to take place.' Contrary to this, the transfer of *social* information, about interactions with third persons, is not allowed. Information

about who helped and who refused, is of course an important resource, but it can only be obtained by personal, direct experience of the helping or refusing behavior of others.

9 Results

The crucial dependent variable is the proportion of cooperators (of either the Commitment type or the Keeping Book Balanced type) in the end populations (S_e) relative to the proportion in the initial populations (S_i). Given the chosen values of the parameters, it will happen that empty end populations emerge. S_e is only computed in case of a non-empty end population. It is only in these cases that new generations emerge.

For applying our results in a multigenerational fashion, the end proportion of cooperators in the present generation is taken to form the initial proportion of cooperators in a new generation. As said, we assume asexual reproduction. The population size is kept constant over generations, assuming that resources are replenished and technology is constant. As long as $S_e > S_i$, the number of cooperators increases over the generations, and as long as $S_e < S_i$, the number decreases. *Equilibria* exist in those cases where $S_e = S_i$.

Obviously the values of S_e differ between different simulations. In order to obtain stable results, we ran 10 series of 50 simulations for each combination of parameter values, and computed the average S_e of the series of 10 average proportions. Each of these 10 averages is computed over its own unique number of surviving end populations.[12]

Results are reported in Figures 3.1 to 3.15. The S_i values are on the horizontal axis and the corresponding S_e values on the vertical axis. Each figure has three curves, one for each value of c. In the following we refer to $c = 0.5q$ as high costs, to $c = 0.25q$ as intermediate costs and to $c = 0.125q$ as low costs. The curves have to be seen as connections of discrete points at which values of S_i and S_e correspond. For easy interpretation we added the diagonal $S_i = S_e$, which represents all possible equilibria. Points above the diagonal represent an increase of S_i in the next generation, points beneath the diagonal a decrease (as said, the S_i of the next generation equals the S_e of the present generation). An increase of S_i between generations means that Commitment players profit more from the

[12] De Vos and Zeggelink (1997) reported mean values and standard errors of 50 repetitions of each different simulation. We replicated their simulations by running ten sets of 50 simulations. Also, we ran 5000 simulations in order to inspect whether the results would differ. This was not the case.

presence of each other than Defectors profit from their presence (Commitment succeeds in excluding Defection). And a decrease of S_i means that Defectors profit more from the presence of Commitment than Commitment players themselves do (Commitment is exploited by Defection). We refer to populations of 10 as small size, to those of 20 as medium-size and to those of 50 as large. If q = 0.2, we speak of harsh conditions, if q = 0.1 of intermediate conditions, and if q = 0.05 of mild conditions.

9.1 Commitment in small populations

How the proportion of cooperators evolves over generations can be deduced from the graphs. For example, the unbroken curve in Figure 3.1, which shows the results for high costs, starts to rise from $S_i = 0.1$ to almost[13] 0.5 at $S_i = 0.2$. This means that one Commitment player entering a small population of Defectors does not survive. But if there are two (with eight Defectors), their proportion increases to almost 0.5. So, in most cases, in the next generation they start with five, together with five Defectors.[14] To find out what happens next, we have to look at $S_i = 0.5$. There we see that S_e is almost 0.7, so that in most cases Commitment starts in the next generation with seven, together with three Defectors.[15] Then S_e is closer to 0.8 than to 0.7, so in the next generation the majority of cases start with eight.[16] There S_e is closer to 0.8 than to 0.9. So in some cases populations with nine Commitment players emerge. The majority of cases reappears with eight, but then contributes again and again to cases with nine. There the curve coincides with the diagonal.

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13 Because the Se values are averages, round proportions almost never appear. Values close to the diagonal were rounded up if they were slightly above the diagonal and rounded down if they were slightly below. The reason for this is that on an evolutionary time scale even a small trend upward or downward in a proportion may result in an increase or a decrease.

14 In the minority of cases that they end up with four, their average end proportion in the next generation is higher than 0.65, which brings the majority of cases to an Si of 0.7. There they 'meet' the cases that reached an end proportion of 0.5 immediately.

15 Because Se is closer to 0.7 than to 0.6 there will be more cases with seven Commitment players in the end populations than with six. In the minority of cases that they are with six, they start with six in the next generation, which brings them to seven in the subsequent generation, the proportion that was reached earlier in the other cases.

16 The minority of cases start again with seven, but then they move up to eight in subsequent steps.

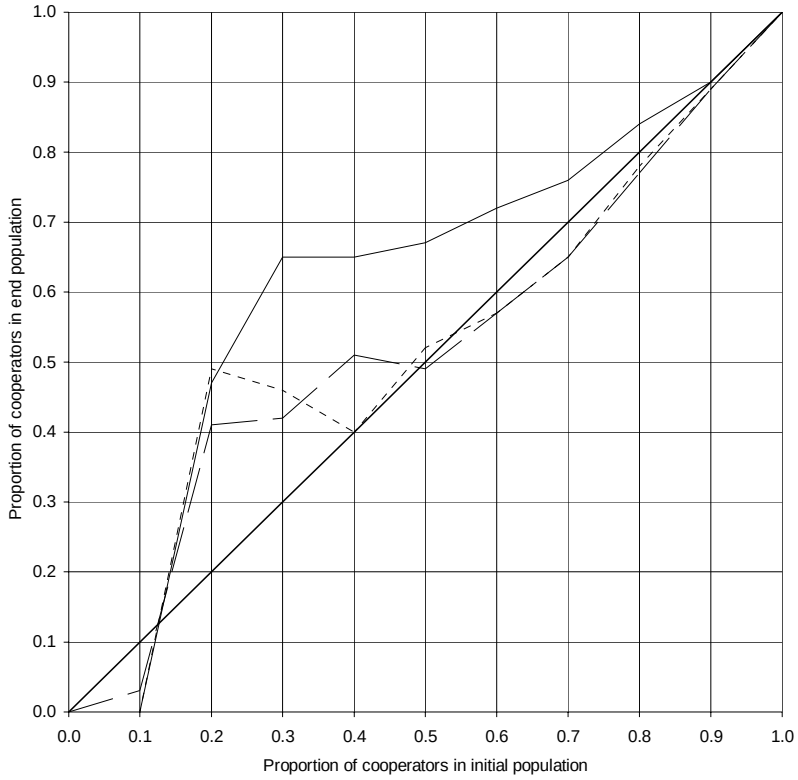


Figure 3.1: Evolution of COMMITMENT in small populations (N=10) and harsh conditions (q=0.2)
Key: —— c=1/2q —— c=1/4q - - - c=1/8q

So in a small population with harsh conditions and high costs of helping, initial populations with two Commitment players and eight Defectors move to an equilibrium of nine Commitment players and one Defector. If it enters with one, Commitment cannot invade a population of Defectors. But a Commitment population can resist an invasion by Defectors.

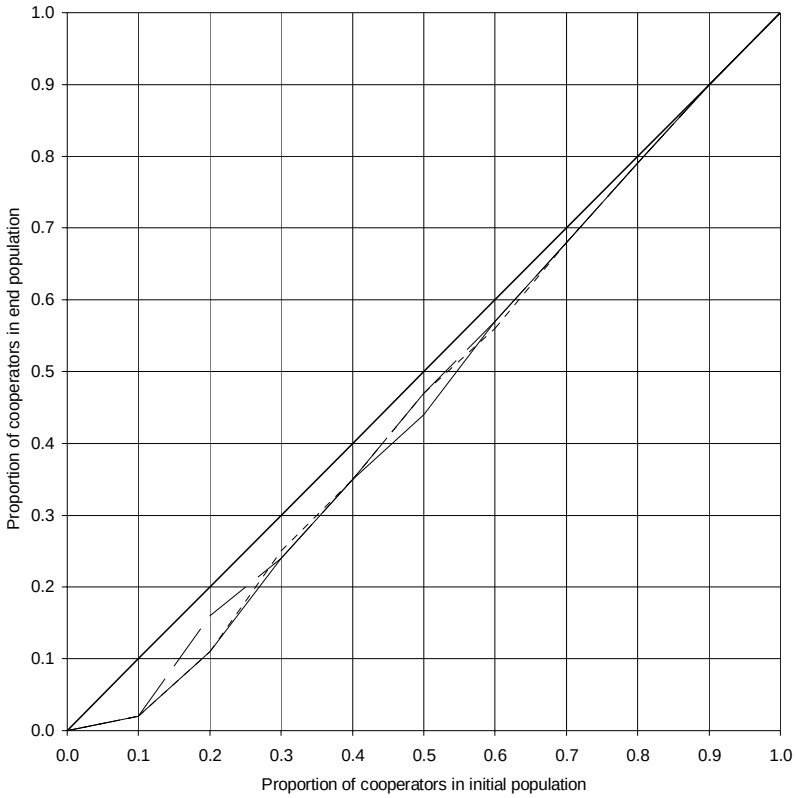


Figure 3.2: Evolution of COMMITMENT in small populations (N=10) and intermediate conditions (q=0.1)
Key: —— c=1/2q —— c=1/4q - - - c=1/8q

Strikingly, Commitment is considerably less successful if the costs of helping are lower. If costs are intermediate, their numbers stabilize at five if they enter with two, three or four. Entering with six, seven or eight, their number falls back to five, and with nine they are able to maintain their number. At the lowest costs there are, aside from $S_i = 0$ and $S_i = 1$, three equilibria, at $S_i = 0.4$, $S_i = 0.5$ and $S_i = 0.9$. The lowest equilibrium is reached only if Commitment enters with four; its number stabilizes at this point. If it enters with two or three, it ends up with five,

just as when it enters with six, seven or eight; if it enters with nine, it again maintains its numbers. So Commitment profits from high costs of helping.

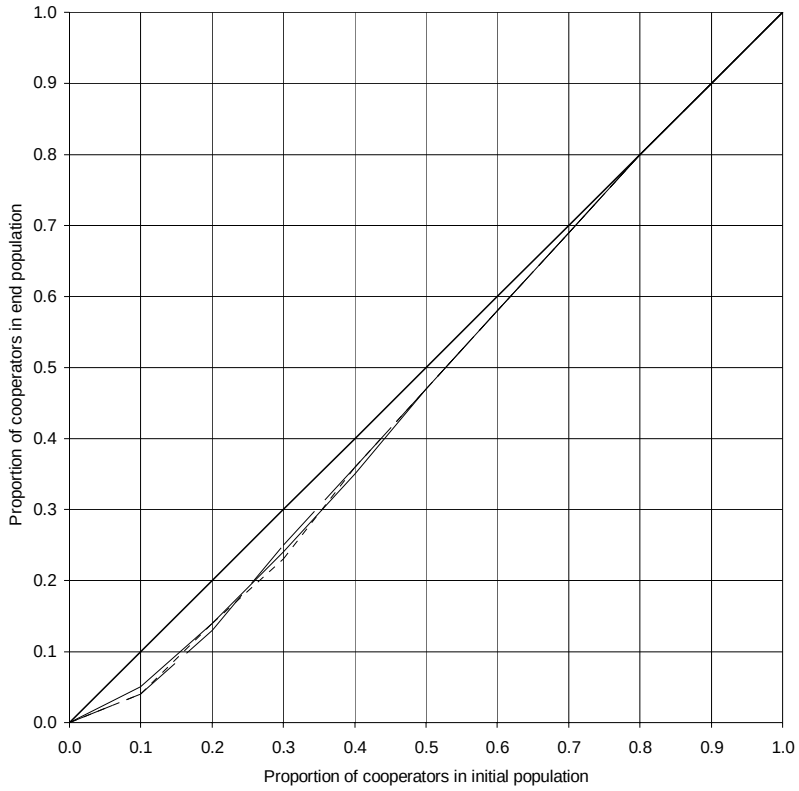


Figure 3.3: Evolution of COMMITMENT in small populations (N=10) and mild conditions (q=0.05)
Key: —— c=1/2q —— c=1/4q - - - - c=1/8q

A plausible explanation is that the frequency of Commitment players' having to ask for help is higher with higher costs of helping. This increases the probability that they find each other, relative to the probability that the Defectors find them.

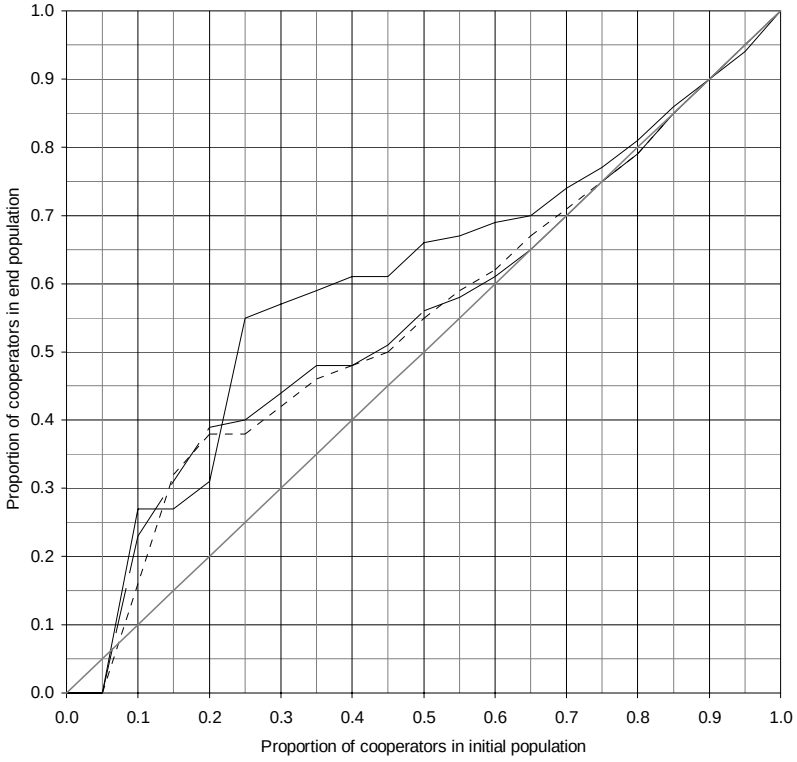


Figure 3.4: Evolution of COMMITMENT in medium-size populations (N=20) and harsh conditions (q=0.2).
Key: —— c=1/2q —— c=1/4q - - - c=1/8q

Figures 3.2 and 3.3 show that less harsh conditions (q = 0.1; q = 0.05) are detrimental to the success of Commitment. In intermediate conditions it can only maintain its number if it enters with nine; in mild conditions it needs to enter with eight. As in harsh conditions, it is able to resist invasion by defectors. The influence of the level of costs of helping has almost disappeared.

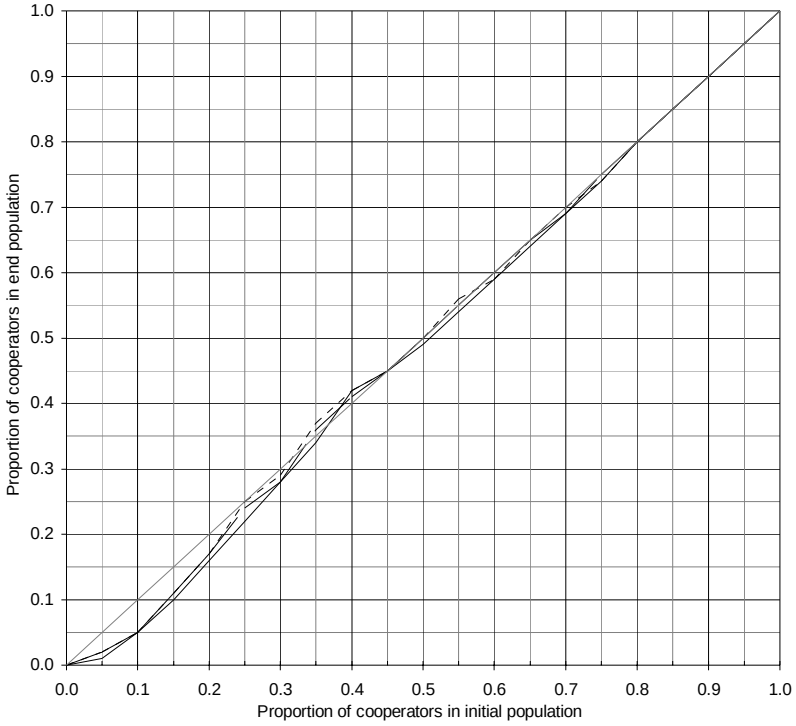


Figure 3.5: Evolution of COMMITMENT in medium-size populations (N=20) and intermediate conditions (q=0.1).
Key: —— c=1/2q —— c=1/4q - - - c=1/8q

9.2 Commitment in medium-size populations

In medium-size populations (initially 20 players) and in harsh conditions (Figure 3.4), we again find that an initial number of two Commitment players ($S_i = 0.10$) is sufficient for an increase, regardless of the level of costs of helping. As in small populations, the increase is strongest in the high-cost condition: it stops at 17 Commitment players and 3 Defectors ($S_i = 0.85$). If Commitment enters with 18

or 19, it is able to resist a further invasion by Defectors. At intermediate and low costs, the equilibrium number is about 14 (S_i = 0.70) if it enters with numbers between 2 to 14. If it enters with more than 14, every initial proportion is an equilibrium; that is, it is able to withstand being invaded. It seems that Commitment profits from an increase in population size, at least with intermediate and low costs of helping.

In intermediate and mild conditions (Figures 3.5 and 3.6) the number of Commitment players decreases at most values of S_i. Only at higher S_i levels do equilibria exist. This pattern is roughly the same as in small populations, with the curves being somewhat closer to the diagonal. In intermediate conditions (Figure 3.5) we even see some small bumps above the diagonal. A striking difference with the small populations is that in intermediate and mild conditions, Commitment does better in medium-size populations than in small ones. As soon as it crosses the minimum threshold (which is high), its proportion increases to 0.7 in large, and to not more than 0.4 or 0.5 in small populations. Apparently, in these conditions a larger population favors Commitment once it has crossed the high threshold.

In sum, if conditions are harsh, in both small and medium-size populations two Commitment players can augment their number but not achieve a complete takeover. In less harsh conditions, Commitment does worse than Defection, except if it enters with large numbers (maintaining its numbers). Costs of helping matter only in harsh conditions, with high costs contributing to the success of Commitment. At intermediate and low costs, Commitment fares better, once it has crossed the minimum threshold, in medium-size populations than in small ones.

9.3 Commitment in large populations

Figure 3.7 shows that in large populations (initially 50 players) with harsh conditions, two Commitment players are again sufficient to allow an increase in their numbers in subsequent generations. With high costs of helping the increase continues until S_i = 0.98, and 49 Commitment players and one Defector form an equilibrium. With lower costs of helping the equilibrium is at S_i = 0.78, if again Commitment enters with at least two.

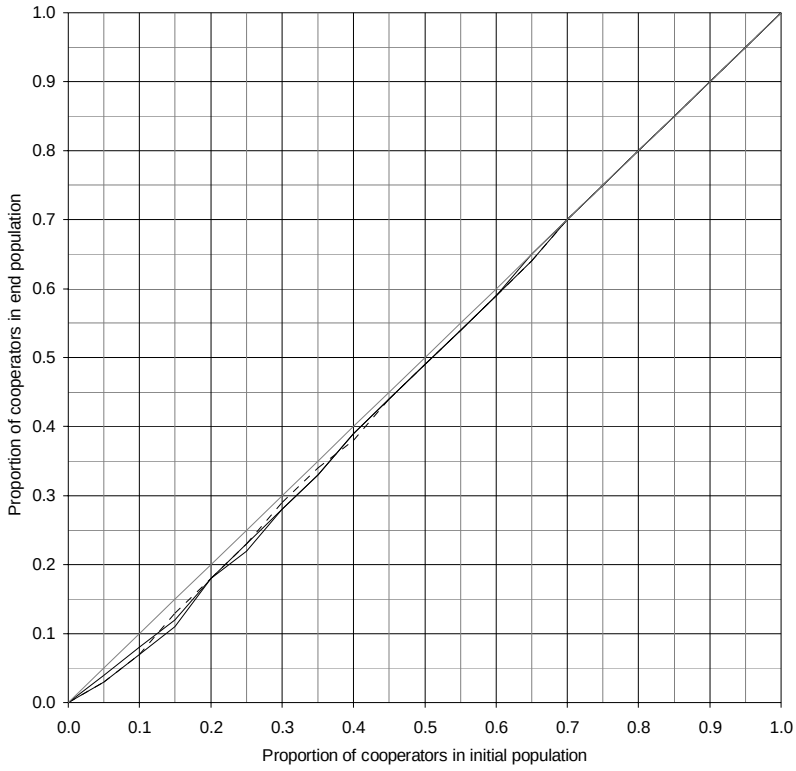


Figure 3.6: Evolution of COMMITMENT in medium-size populations (N=20) and mild conditions (q=0.05).
Key: —— c=1/2q —— c=1/4q - - - c=1/8q

In intermediate conditions (Figure 3.8) the curves are closer to the diagonal. Nevertheless there are many more values of S_i at which they are above the diagonal than in the same conditions in medium-size and small populations. An increase of Commitment players starts from about $S_i = 0.16$ - that is, if they enter with eight -and ends at about $S_i = 0.56$, when they number 28, almost independent of the level of the costs of helping.

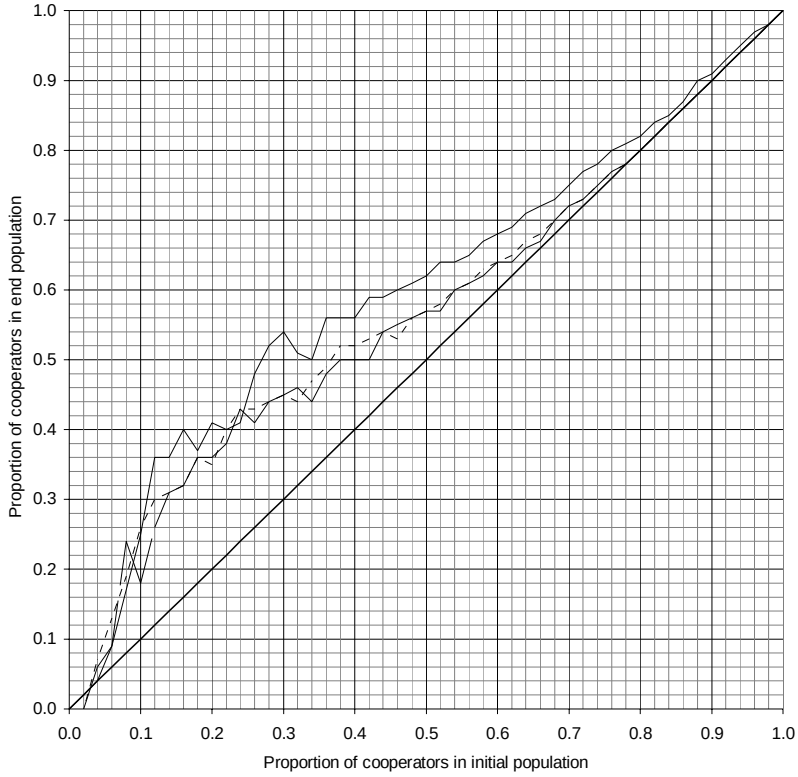


Figure 3.7: Evolution of COMMITMENT in large populations (N=50) and harsh conditions (q=0.2)
Key: —— c=1/2q —— c=1/4q - - - - c=1/8q

In mild conditions (Figure 3.9) the curves closely follow the diagonal; that is, many S_i values represent an equilibrium.

We summarize the results for Commitment in competition with Defection. Commitment *invades a population* - that is, profits more from its own presence than Defection does - as soon as it enters with two:

1) in small and medium-size populations: if conditions are harsh,
2) in large populations: if conditions are harsh or intermediate.

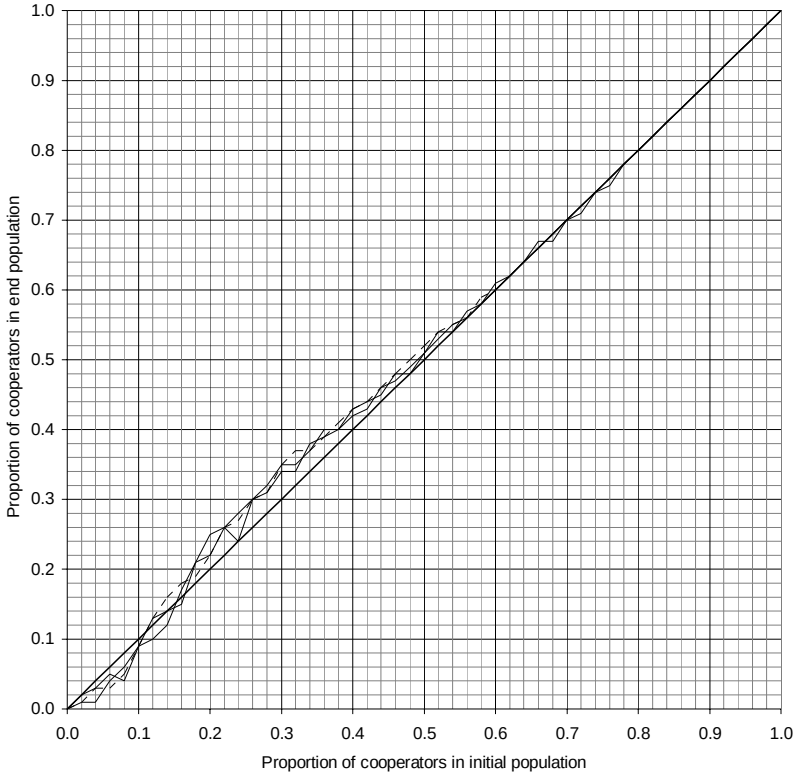


Figure 3.8: Evolution of COMMITMENT in large populations (N=50) and intermediate conditions (q=0.1)
Key: —— c=1/2q —— c=1/4q - - - c=1/8q

Commitment is able to resist an invasion by Defection:

1) in a small population, if conditions are harsh and the costs of helping are high,
2) in a medium-size population, if conditions are harsh irrespective of the level of costs,
3) in a large population, irrespective of harshness of conditions and of the level of costs.

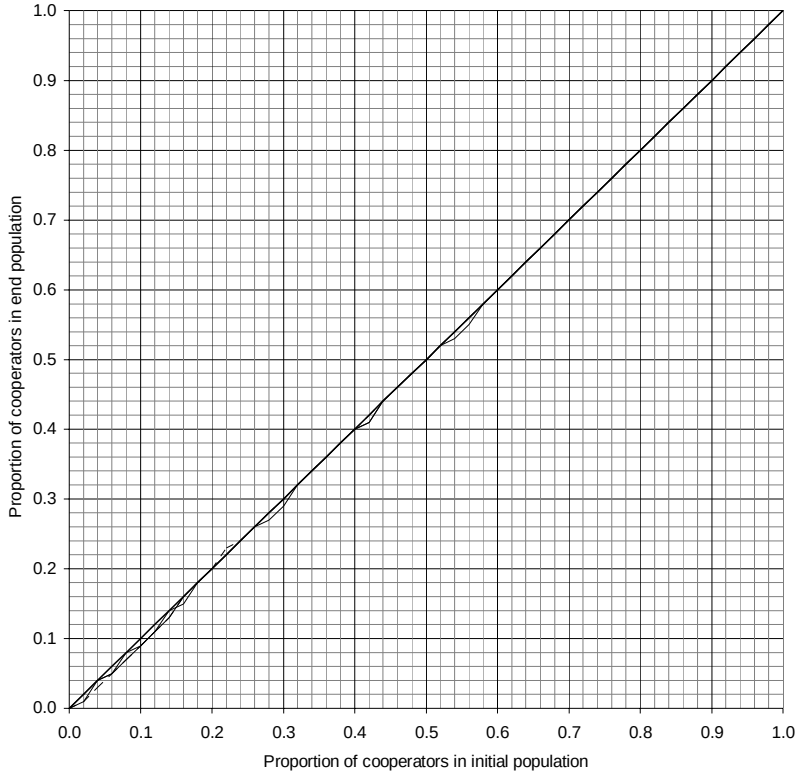


Figure 3.9: Evolution of COMMITMENT in large populations (N=50) and mild conditions (q=0.05)
Key: —— c=1/2q —— c=1/4q – – – c=1/8q

Commitment seems not to be bothered by high costs of helping, and even seems to be favored by high costs. For harsh conditions, the level of costs does not matter for Commitment's ability to increase its numbers if it enters with two. And if it enters with a majority, it is better served with a high level of costs. In a small population, low costs even cause a decrease of Commitment players.

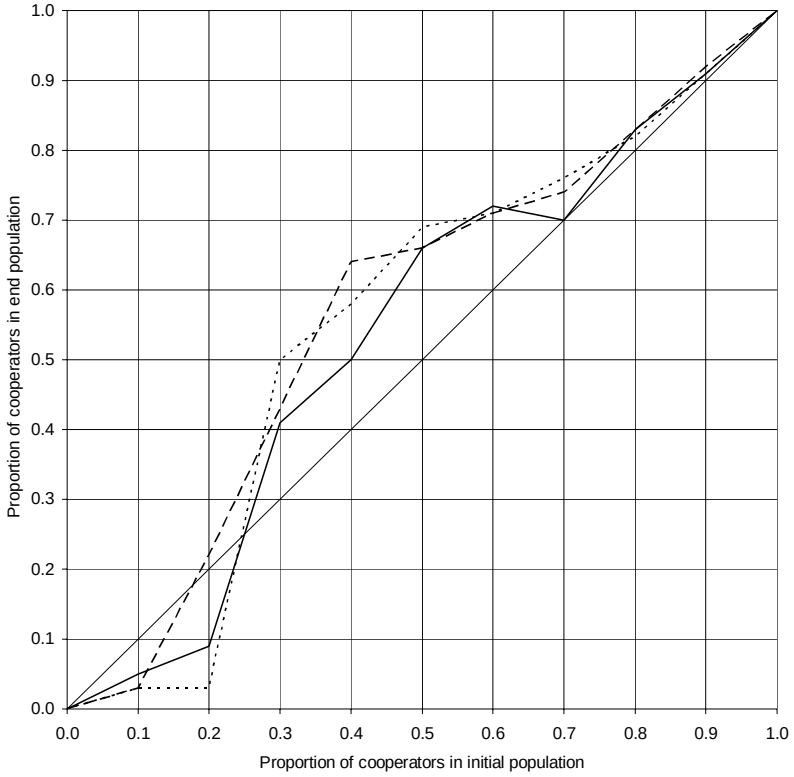


Figure 3.10: Evolution of KEEPING BOOKS BALANCED in small populations (N=10) and harsh conditions (q=0.2)
Key: —— c=1/2q – – – c=1/4q ····· c=1/8q

9.4 The success of Commitment relative to Keeping Books Balanced

To examine the success of Commitment relative to Keeping Books Balanced, we compare our results with our replications of the simulations of De Vos and

Zeggelink.[17] Comparison is possible only for small and medium-size populations. Figures 3.10 to 3.15 show the results for Keeping Books Balanced.

In one respect the two results are very similar: the cases in which reciprocal altruism is successful are restricted to harsh conditions. Nevertheless, in these conditions there are important differences in the degree and the pattern of success. Before we describe these differences, we deal with the mild and intermediate conditions. In these conditions both strategies fare worse (or, if they are numerous, just as well) as Defection (compare Figures 3.2 and 3.3 with 3.11 and 3.12 and Figures 3.5 and 3.6 with 3.14 and 3.15). Commitment is more successful than Keeping Books Balanced in medium-size populations: it needs fewer numbers to reach an equilibrium.

Although both strategies need an environment in which help is often required, to be a successful line of conduct in competition with Defectors, there are also important differences between them in these harsh conditions. Comparing the results for small populations (Figures 3.1 and 3.10), we observe that whereas Commitment needs to enter with only two, Keeping Books Balanced needs three to augment its numbers. So, Commitment has a lower threshold for invasion. But we also observe that Keeping Books Balanced, if it has crossed this threshold, takes over the population, except for one mixed equilibrium if costs are high. Commitment, with its lower threshold, produces more mixed equilibria: 0.9 if costs of helping are high, and still lower ones if costs are intermediate or low. Commitment enters easier, but once in the population, it is less successful in taking over. There is a striking difference between the effects of the level of costs of helping. Commitment clearly profits from high costs, whereas the level of costs does matter much less, with high costs being more *unfavorable*, for Keeping Books Balanced. Moreover, if costs are intermediate or low, Commitment achieves *worse* than Keeping Books Balanced, that is, the invasion ends at lower proportions.

[17] Note that the comparison is made with our replications, using 500 simulations for each parameter combination; not with the results reported by De Vos and Zeggelink (1997). However, both results have very much the same pattern. Most differences are found with small values of Si, which is no surprise considering the small amount of surviving populations with these values.

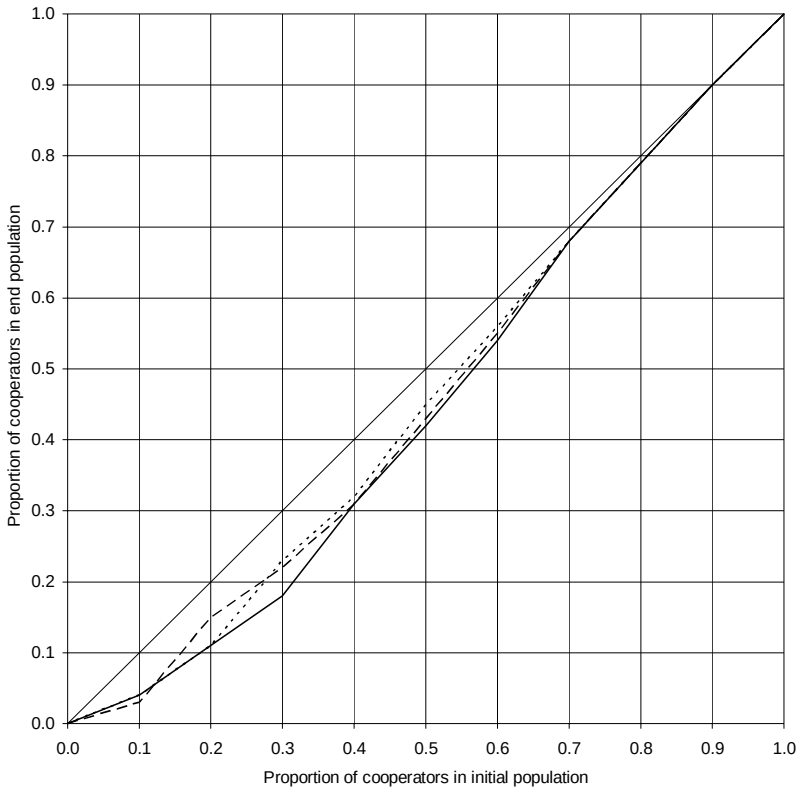


Figure 3.11. Evolution of KEEPING BOOKS BALANCED in small populations (N=10) and intermediate conditions (q=0.1).
Key: —— c=1/2q – – – c=1/4q ····· c=1/8q

For medium-size populations we compare Figures 3.4 and 3.13. In Figure 3.13 we observe that for values of S_i lower than 0.2, the pattern of outcomes is unclear. If starting with one, Keeping Books Balanced tends to increase with low and intermediate costs and to decrease with high costs; starting with two, the success in cases of low and intermediate costs decreases dramatically, but if costs are high, the outcomes meander around the diagonal. These fluctuating results are a consequence of the low number of populations that survived, making the results vulnerable to chance hits. Above $S_i = 0.15$ the results are more stable. Comparing

with Figure 3.4, we observe that again, Commitment is more successful than Keeping Books Balanced, especially with high costs of helping. First, the threshold for increase of its numbers is only two ($S_i = 0.10$) for Commitment and four ($S_i = 0.20$) for Keeping Books Balanced, irrespective of the level of costs.

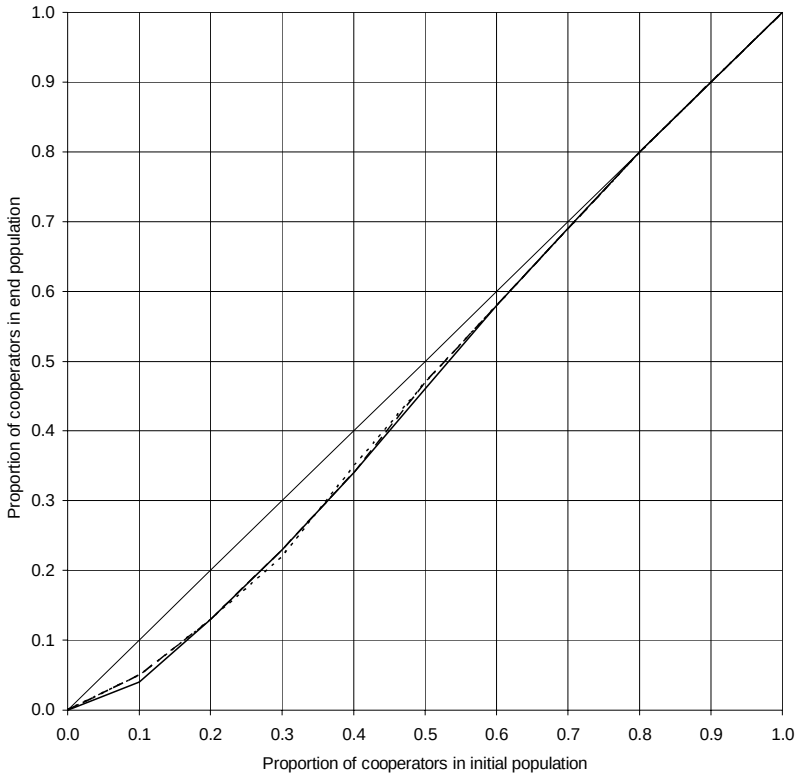


Figure 3.12: Evolution of KEEPING BOOKS BALANCED in small populations (N=10) and mild conditions (q=0.05)
Key: —— c=1/2q – – – c=1/4q ····· c=1/8q

And second, once the threshold has been crossed, the equilibria that arise are at much higher S_e values for Commitment than for Keeping Books Balanced, again irrespective of the level of costs. Although the level of costs matters for Commitment, even if this level is 'unfavorable' to it (low or intermediate costs), it still achieves *better* than Keeping Books Balanced, which is in contradistinction to the effect of costs in small populations.

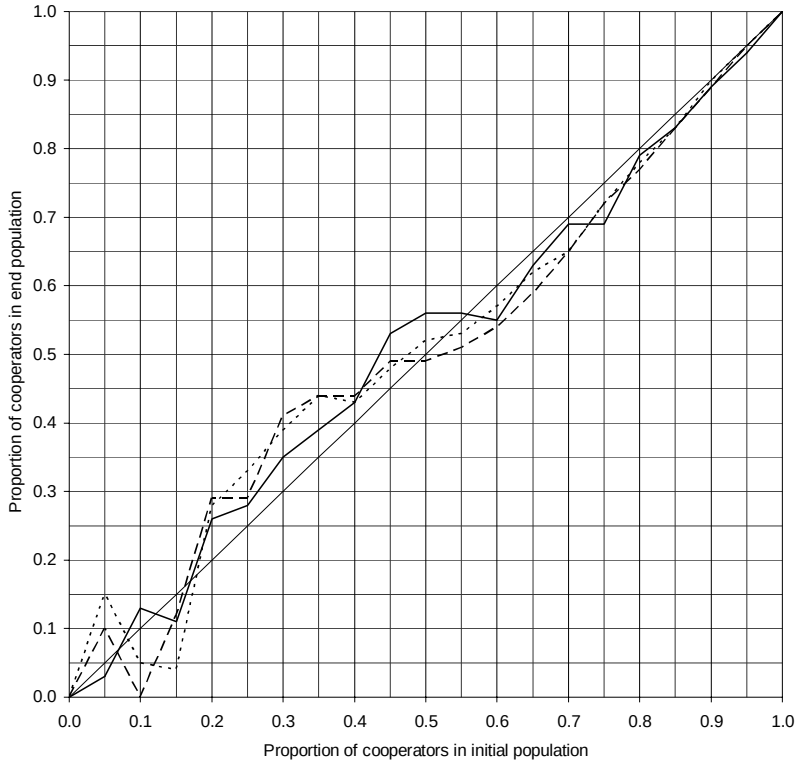


Figure 3.13: Evolution of KEEPING BOOKS BALANCED in medium-size populations (N=20) and harsh conditions (q=0.2).
Key: —— c=1/2q – – – c=1/4q ····· c=1/8q

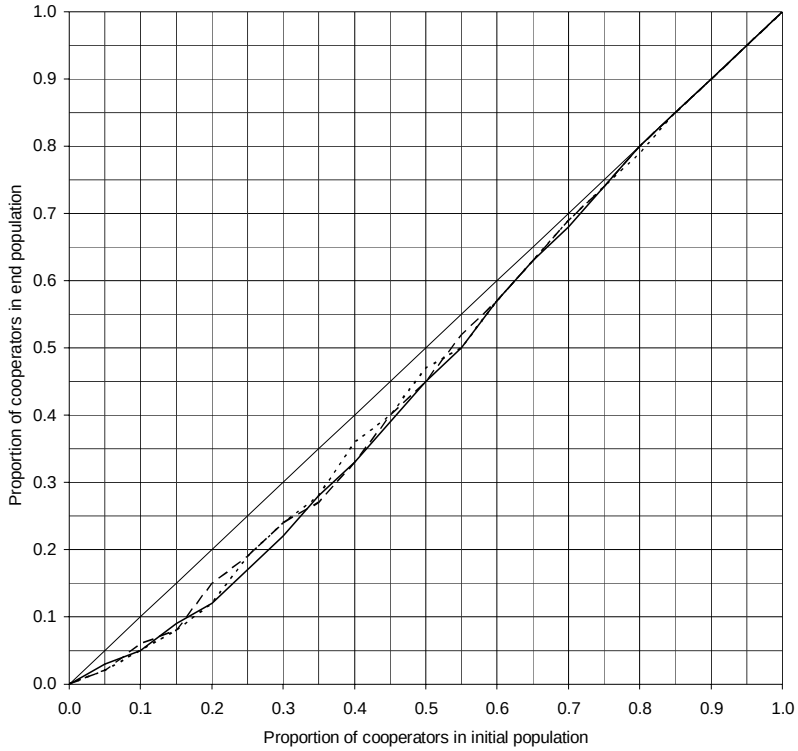


Figure 3.14: Evolution of KEEPING BOOKS BALANCED in medium-size populations (N=20) and intermediate conditions (q=0.1).
Key: —— c=1/2q – – – c=1/4q ····· c=1/8q

We summarize the main results of the comparison.

1) In intermediate and mild conditions both strategies need to enter with large initial majorities in order to maintain their numbers, although in medium-size populations Commitment is more successful than Keeping Books Balanced.
2) In harsh conditions, the threshold for an increase is lower for Commitment than for Keeping Books Balanced.

3) In harsh conditions, the threshold proportion for Commitment is not influenced by population size (for the two sizes we examined), contrary to the threshold proportion for Keeping Books Balanced, which is higher in the medium-size populations.
4) In all conditions the two strategies are equally able to resist an invasion by defectors.

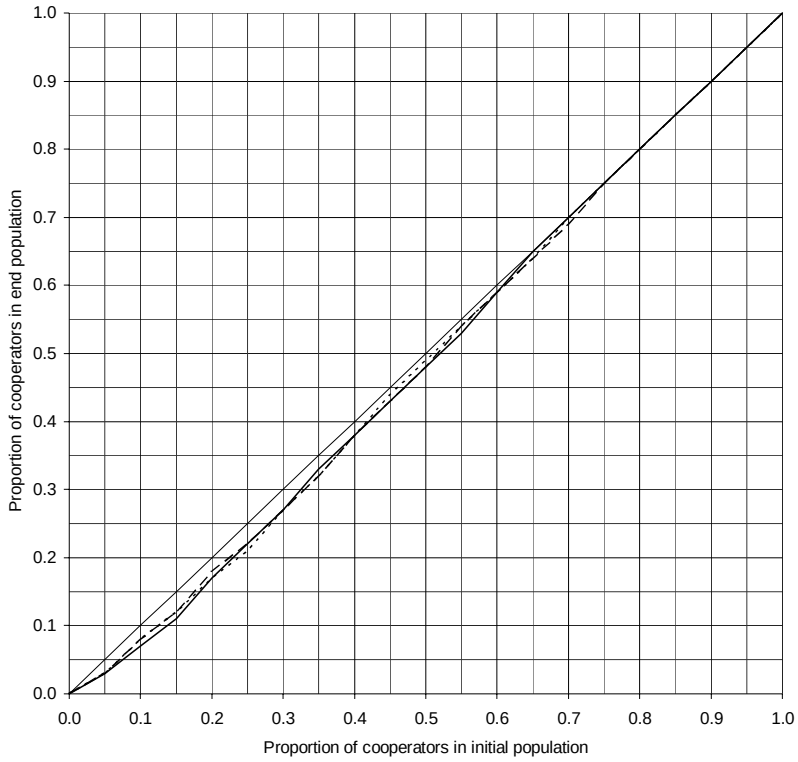


Figure 3.15: Evolution of KEEPING BOOKS BALANCED in medium-size populations (N=20) and mild conditions (q=0.05).
Key: —— c=1/2q – – – c=1/4q ····· c=1/8q

5) Commitment is favored by high costs of helping, whereas costs do not matter for Keeping Books Balanced, or, if it matters, it is favored by low costs.

10 Discussion

Theoretically the most interesting aspect of our results is how they relate to whether cooperators are able to invade a population of defectors.[18] As the SEM allows for clustering taking place as a consequence of the actions of the cooperators, one of our main interests was the minimum number with which the cooperators need to enter in order to increase their number, resulting in a complete takeover or not (the threshold for invasion). The second main point of interest was the ability of the cooperators to take over the population. We also dwell on the issue of interpretation of the two strategies and we conclude with mentioning some limitations of this study.

The threshold for invasion

Neither of the two reciprocal altruistic strategies we examined is able to invade a population of defectors if they enter one at a time. With both strategies, the vulnerability of the first reciprocal altruist to exploitation by defectors is high. Nevertheless, it appears that for Commitment an initial number of two is sufficient for an invasion if conditions are harsh. This is even the case in large populations. We think that Commitment's having such a small threshold for entering and evolving (in harsh conditions), is an important finding.[19]

Still, even for Commitment the threshold is larger than one. Given the extremely small probability of having two Commitment mutants at the same time in one and the same population, should it not be considered impossible for such a strategy to enter *and* evolve? This obstacle to proliferation may be smaller than it appears from our results. It has to be noted that the vulnerability of the lonely Commitment player is above all a consequence of the peculiar fact that the defectors start to exploit her as soon as she enters the scene. This is a consequence of the even more peculiar fact that they ask for help without even one reciprocal

18 Both cooperative strategies were able to resist an invasion by defectors.

19 Also, due note should be taken of the fact that in a very small number of simulations a lonely cooperator survives, and then immediately produces a high proportion of cooperators in the next generation.

altruist present. If we would remove this peculiarity, than it is only with the entering of at least one reciprocal altruist that a social environment emerges in which a selection for asking help, and for exploitation, could take place. The probability that all, or even one of the defectors, had acquired this trait by way of mutation, just when the first exploitable player enters is probably extremely small. So, in the simulations Defection was, after all, unrealistically smart in exploiting the first Commitment player that enters.

Nevertheless, due note should be taken of the precise nature of this result. The success of the two Commitment players must be a consequence of their sometimes finding each other in the first round when one of them gets in need. After this event their relationship will flourish. How improbable is this event? In each round there are three opportunities to find a benefactor. Consider a complete population of 10, with two Commitment players, and one of the two experiences the first round of distress. Then, if he is the only one who is in need, the probability that he perishes at the end of this round, equals the probability of not finding his 'comrade' at the first, and not finding her at the second, and not finding her at the third opportunity. This equals (8/9) x (7/8) x (6/7) = 0.67. In a population of twenty, with the same assumptions, this probability increases to 0.84, and in a population of fifty to 0.94. These are, however, only the lowest possible values, because we assumed that none of the defectors got in distress. If we drop this assumption, it can happen that his 'comrade' is also asked for help by one or more of the defectors. This further increases the probability that he perishes, because help might go to a defector. And, finally, things are even worse, because if the two comrades' first time of distress happens in the same round, both perish. So, in by far the most cases the two Commitment players do not succeed in surviving the first round in which at least one of them needs help.

However, we must keep in mind that the S_e values are mean values, resulting from 50 simulations of which only those with at least one survivor were used to calculate these values. In the small number of those simulations that the two Commitment players found each other, they formed a happy couple with a considerably increased probability of survival. Finding each other is also very detrimental to the defectors, because from then on they are less available to be exploited. Therefore, although the two Commitment players were unsuccessful in most cases, in the few cases that they succeeded, their success in terms of their proportions in next generations was overwhelming, relative to the fortunes of the Defectors. So the fact that Commitment enters more easily than Keeping Books Balanced does not necessarily mean that, entering with two, it succeeds in more

cases, but rather that it is much more successful in the few cases in which it does succeed.

That a few numbers of Commitment players are more successful as soon as they find each other than a few numbers of Keeping Books Balanced players must be a consequence of their being better able to take advantage of each other's presence *after they have found each other*. But this is not the only way in which the success of Commitment is increased. Compared with a Commitment player, a Keeping Books Balanced player suffers from two bad habits. First, she meticulously keeps scores of help provided and help received, always trying to be even with every single other player. This contributes to her vulnerability, because she wastes opportunities to find a helping partner by repeatedly trying to get even with the Defectors whom she once helped. But second, she refuses to help a 'comrade' (that is, another Keeping Books Balanced player) with whom she exchanged help in the past and who happens to be in her debt in that particular round. Her behavior thus contributes to the shortening of the other's life, which is detrimental to herself. Commitment is more sophisticated because it is not only good in profiting from the presence of other cooperators, but *also in contributing to their survival as soon as they have found each other*, so that they continue to be present as providers of help in the future.

As a consequence of the popularity of the Prisoner's dilemma game paradigm, attention has been given almost exclusively to cognitive and emotional adaptations that enhance cheater-detection abilities and prompt retaliation (Cosmides and Tooby 1992, Frank 1988). These abilities indeed are important, given that you are forced to interact with others, and only then are you able to select your actions, instead of being able to select your interaction partners and at the same time your actions towards them. Commitment can be seen as a cognitive-emotional adaptation to an environment in which you have to select your interaction partners all by yourself, and in which your survival and reproduction depend on your propensity to stick to the partners who have proven their goodwill (see also the section on the interpretation of commitment below). This kind of adaptation does not receive much attention as long as partner selection behavior is not systematically studied as a possibly important contribution to cooperation.[20]

[20] In the Prisoner's Dilemma game studies with a kind of partner selection (Hayashi and Yamagishi 1999; Watanabe and Yamagishi 1999; Yamagishi et al. 1994) there is no comparison between (cooperative) strategies with varying degrees of commitment. For example in Watanabe and Yamagishi (1999) every player, independent of its strategy, moves toward another player who cooperated and moves away from another player who defected (the distance toward another player determines the probability of selecting this player).

It should be emphasized that Commitment's low threshold for invasion was only found in the harshest conditions that we examined. In fact, what we found is that Commitment needs extremely harsh conditions for its evolvement.

We explicitly draw attention to the fact that such a thing as harsh conditions did not emerge as a determining variable from studies using the iPD. The commonplace intuition that reciprocal altruism should be an important asset in a risky environment,[21] could not easily be considered in these studies. The players in the PD game simulation studies are never confronted by the vicissitudes of nature. What happens to them is that now and then, for some reason, they have to play this peculiar game with some other player.

We do not claim that commitment cannot be studied within those PD studies that allow for partner selection (see Hayashi and Yamagishi 1999; Watanabe and Yamagishi 1999; Yamagishi et al. 1994). But the SEM has some clear advantages. The nonsimultaneity of exchange makes it a more realistic model for studying a kind of cooperation that is pervasive in human interaction. In the selective play PD simulations, players select another player for playing a PD. This means that there is an actual play only if two players select each other, which often does not happen. This makes the matching of players cumbersome and artificial. Also, the SEM allows for (easy) modeling of degrees of harshness of natural conditions. Because of these differences, the meanings of the two concepts of commitment do of course also differ (see also below).

The ability to take over the population

In the harsh conditions and if costs are high, once the threshold for invasion has been crossed, Commitment almost takes over the population. The finding that Commitment's ability to take over is thwarted by a decrease of the costs of helping, most clearly in the small populations, is striking. The ability of Keeping Books Balanced to take over the population is not influenced by the level of costs of helping, or, if this influence seems to exist, in the small populations, it is in the opposite direction. An increase in the costs of helping enhances the probability that Commitment players find each other, which has a larger-than-commensurate effect on their average proportions in the surviving end populations. The increase of costs of helping does favor their *relative* survival, because the higher probability of their finding each other is very detrimental to the survival of the defectors.

[21] Risky in the sense that there is no food production and storage and resources are scarce and patchily spread.

How to interpret Commitment?

The 'concern' of the Commitment cooperators for each other's survival, suggests an interpretation as a *cognitive-emotional adaptation* that tells the individual to *appreciate intrinsically* the relationship he has with other individuals from whom he received help in the past.[22]

In the framework of the principle of hierarchical organization of behavior, emotions, and the aversions and desires linked up with them, are intermediate goals to inclusive fitness, that don't need conscious calculation for being effective in regulating behavior (Frank 1988; Miller et al. 1960; Plotkin 1994; Sober and Wilson 1998; Tinbergen 1951). We tend to interpret commitment as an extension of the more ancient *attachment* emotion, that is directed to the primary caretaker and contributes to inclusive fitness because it enhances the probability of receiving care (Bowlby 1982). Just as attachment is a kind of complement to kin altruism, commitment, then, would be an emotion that is indissolubly connected with reciprocal altruism. To keep profiting from reciprocal altruistic relationships, you need to feel committed to those others who showed their goodwill, probably in the sense of the Commitment strategy. You feel motivated to be benevolent to your benefactors, not because the resulting behavior is 'rational', but because your ancestors were selected for having this emotional mechanism.

Gouldner formulated a weaker version of commitment in his neglected paper on the universal 'norm of reciprocity'. He describes this norm as making two minimal demands: (1) people should help those who have helped them, and (2) people should not injure those who have helped them (Gouldner 1960, p. 171). The requirement of not injuring is weaker than of contributing to your partner's survival.

We speculate that the ancestors of modern humans were selected for an ability to appreciate a delayed exchange relationship as a value in itself, an affect-laden social bond, for the maintenance of which it is worth to make sacrifices. There is overwhelming evidence for contemporary humans' valuing relationships that provide companionship and support in times of stress (Cohen and Wills 1985, Rook 1987, Rook and Pietromonaco 1987), and for their abilities and dispositions to function in relationships in which partners are concerned about each other's welfare (Halpern 1997; Mills and Clark 1982). Also, human friendship intensity was

[22] Our concept of commitment differs from the way Frank (1988) uses the same term. Commitment in his sense means that a person is emotionally bound to a line of conduct, and involuntarily communicates this, towards others. In our sense, commitment is an emotional attachment to a person from whom help was received, that can be interpreted as the emergence of the relationship with this person as an object valued in itself.

shown to be more highly correlated with a benefits-plus-costs score than with a benefits-minus-costs score (Hays 1985), which suggests that people positively value the making of sacrifices in a personal relationship.

We think that our study also points to the relevance of the distinction made within *social exchange theory* between economic exchange and social exchange (Blau 1989, Ekeh 1974). The primacy of commitment in our interpretation would be characteristic for social exchange, whereas the primacy of cheater detection would be typical for economic exchange. Kollock (1994) and Lawler and Yoon (1993, 1996, 1998) report experimental results that support our interpretation. Kollock found that his subjects had a tendency to remain with an exchange partner despite better offers from other potential partners. Although this tendency was highest when change of partners could involve staking future benefits, it was also present in conditions in which no risk was involved. Kollock therefore suggests that "commitment will be present to some degree in any exchange system" (1994, p. 335). Similar results are reported by Lawler and Yoon, who formulated and tested a theory of relational cohesion that asserts that frequent exchanges between two actors in a network make their relation an expressive object, valuable in its own right, because mild, positive emotions are produced by successful exchanges (1996, p. 89).

Finally, in the field of *social support theory* there is a lot of evidence that people suffer negative physiological and health consequences if relationships are lacking in which partners are concerned for each other's welfare (Schwarzer and Leppin 1991; Uchino et al. 1996). This evidence supports suggestions that relationships may have an element of emotional attachment, that they are important to people for non-instrumental reasons (Pearlin 1985), and that the mere existence of such relationships is rewarding (Levinger and Huesmann 1980).

An interesting issue is how the SEM, and the results of this study, relate to the problem of the emergence of generalized exchange or so-called pure altruism.[23] Takahashi (2000) showed that generalized exchange (A helps B and at a later moment help is 'returned', but by C instead of by B) can exist if players with a 'gene' for this kind of exchange make their giving conditional on the recipient's behavior towards others and if they have a sense of fairness. His results lean heavily on the assumption that all actors of the population, or of subgroups, know each others' behaviors. This means that some kind of initial (sub)group formation is introduced by assumption. In the SEM, 'generalized exchange' can arise quite

[23] This issue, and the one mentioned in the following paragraph, were suggested by one of the reviewers.

naturally within the *emerging* groups of cooperators (see also the section on the limitations of this study).[24]

Another relevant issue is how Commitment relates to the Out-for-Tat (OFT) strategy that was successful in the computer tournaments using the selective play PD paradigm, reported in Hayashi and Yamagishi (1998). Participants of these tournaments had to decide about an action strategy (for acting in a PD) and about a selection strategy (for selecting partners to play a PD with). The OFT-player (1) always cooperates (that is, the action strategy is unconditional cooperation); (2) sticks with the current partner insofar as the partner cooperates, and (3) deserts the partner as soon as the partner defects. This makes OFT very similar to Commitment, although we have to realize that comparison is difficult because of the different restrictions and environmental conditions. Although OFT was successful, its performance strongly decreased when 'opportunity costs' were introduced. This was done by assigning each pair of players a unique asymmetric PD payoff matrix, so that sticking with a cooperative partner could mean that better partnerships were ignored. In this condition it paid to (1) remain unconditionally cooperative, (2) be cool, in the sense that in selecting partners you should pay attention only to outcomes, not to whether your partner is cooperative, and (3) have a high level of trust towards strangers - that is, players with whom you have never interacted. It is quite difficult to ascertain the implications of the differences between this tournament environment and the SEM. Nevertheless, a preliminary conclusion could be that these results point to an readily observable weakness (see again the section on the limitations of this study) of Commitment, namely that it lends itself to exploitation by a defector who helps now and then. In that case, sticking with a partner who helped only once wastes time that is badly needed for finding a 'real' benefactor. But we should also realize that the SEM in its present form is designed for studying situations in which finding help as a response to a life-threatening need is immediately of vital importance. This makes looking for still better alternatives a risky thing to do if you have already found a cooperative partner.

Limitations of this study

Although we believe that the results of this study are of importance to the problem of how cooperation could have evolved in human evolution, it has some clear limitations. In the first place, Commitment has one clear inconsistency. Although

[24] Group formation within the SEM was studied by De Vos and Zeggelink (1994) and Zeggelink et al. (2000).

the Commitment cooperators were considered able to exchange information about the natural environment, as one possible form of help exchange, they were not 'allowed' to exchange *social information*, that is, information about which third party has been willing to help in the past. Thereby we also did not 'allow' *generalized reciprocity* to evolve, which probably would have favored the selection for Commitment.

On the other hand, we also fixed the nature of Defection. Given the presence of Commitment, a defecting strategy that is just a little bit more sophisticated, one that provides help now and then, most probably would have fared much better in exploiting Commitment. In fact, the process that we simulated should be seen as not more than just the initial level of a kind of *evolutionary arms race* of increasingly advanced cooperative and defecting strategies.

CHAPTER 4

Reciprocal altruistic behavior in dilemma situations. Helping as a response to a need or scorekeeping?[1]

1 Introduction

What would you do if someone you didn't know so well – let's say a vague acquaintance – repeatedly asked you for favors? Most probably, it should not take long before you would start to feel exploited: being just an acquaintance he should reciprocate your favors. But what if this person were a friend? In that case you would probably be drawn between two considerations: on the one hand, *he is a friend, and he needs my help, so I should help him*. But on the other hand, there might be some degree of entitlement: *he is in my debt and people should repay their debts*.

The idea that the providing of benefits is organized by different relational models, depending on who is the recipient of the benefits, has been subject of both theoretical accounts and empirical studies. Clark and Mills (1979) distinguish between *exchange relationships* and *communal relationships*. Communal relationships are characterized by mutual concern about each other's welfare and a positive attitude towards benefiting the other when a need exists. Exchange relationships, on the other hand, are characterized by the obligation to reciprocate a received benefit with a comparable return benefit. Clark and Mills hypothesize that individuals have communal relationships with family members, romantic partners and friends, whereas relationships with acquaintances, strangers and business partners pertain

[1] This chapter has been submitted for publication (co-authored with Henk de Vos and Bram P. Buunk).

to the domain of exchange relationships. The results of their experiments demonstrate that towards (potential) friends or romantic partners, subjects are less likely to keep track of benefits provided and benefits received, and show more liking if the other does *not* keep tracks of benefits provided and benefits received, than towards strangers or persons who are not available for friendships or romantic partnerships (see also Clark 1984). Deutsch (1975) distinguishes between different norms of distributive justice. The equity norm, according to which a person's received benefits should be proportional to the costs he has made, is very suitable to describe the operation of exchange relationships. In contrast, the need norm, according to which a person should be rewarded according to his needs, is apt to describe the workings a communal relationships. In a study by O'Connell (1984), the presence of different norms governing exchange behavior was tested among people who build their own houses. The results show that benefits exchanged between kin and friends, in contrast to benefits exchanged on the market-place, are governed by non-instrumental concern and the need norm.

Similar distinctions can be found in a number of theoretical accounts. Fiske (1992) proposes four universal forms of sociality, of which *communal sharing* is identical to Clark and Mills' communal relationship, whereas both *equality matching*, in which people keep track of the imbalances among them, and *market pricing*, where all relevant features and components are reduced to quantitative utilities, can be considered as part of Clark and Mills' exchange relationship. Lindenberg (1988; see also Lindenberg 2000) distinguishes between s*trong solidarity* and *weak solidarity* relationships. Strong solidarity relationships are similar to communal relationships to the extent that there is a focus on the common interest and on the equality of the individuals involved; weak solidarity relationships are similar to exchange relationships to the extent that they are characterized by individual gain and a direct correlation between one's investments and one's rewards. Additionally, Weiss (1998) distinguishes between *attachments*, which are characterized by the perception of the other as a secure base, and *affiliations*, in which the aim is to advance a common interest. The distinction between these two types of relationships can be traced back to older discussions within the social sciences in which models recognizing the importance of social needs and motivations were offered as a reaction to the economic models of purely self-interested individuals (Blau 1964; Ekeh 1974; Homans 1974).

As long as the situation is unambiguous, the distinction between communal and exchange relationships is non-problematic. If persons are in a communal relationship, they help each other without expecting a future return. On the other hand, if they are in an exchange relationship, they expect their benefits to

be reciprocated by comparable benefits. As soon as the situation is less unambiguous, however, containing characteristics of both communal and exchange relationships, the theory does not predict how people will behave. For example, how to behave towards business partners who are also friends? Or how to respond to a friend who asks for help over and over again? Many studies have addressed the question of how friendship affects economic transactions. On the one hand, a minimal amount of friendship between business partners is necessary, in the sense of trust in each other's intention not to exploit each other (Gulati 1993; Macauley 1963). On the other hand, friendship considerations hamper economic interests (Lindenberg 2000; Uzzi 1997). Experiments have shown that in transactions with friends, sellers ask lower prices and buyers offer higher prices than in transaction with acquaintances or strangers (Halpern,1997; Ligthart 1995).

Notwithstanding the empirical interest in communal and exchange relationships, both in unambiguous and in ambiguous situations, a theoretical background seems to be lacking. The distinction between communal and exchange relationships is mostly based on empirical and common sense considerations. Furthermore, little attention is given to the question what is actually happening on a cognitive level when people are confronted with a conflict between communal and exchange considerations. An exception is formed by Lindenberg's framing theory, which states that an individual's behavior is dependent on the relative salience of an array of goals or "frames" that can switch back and forth to the centre of one's attention (Lindenberg 2001). Although Lindenberg distinguishes between a limited number of master frames that differ in relative a priori strength (p. 601), a theory from which the frames are derived is lacking. In the next section, we show that (1) evolutionary psychology provides a theoretical basis for the distinction between communal and exchange relationships, and (2) serves as a theory for assigning priorities to the different relational models in ambiguous situations.

2 Evolutionary psychology of exchange and communal behavior

According to evolutionary psychology humans are equipped with specific *mental modules, or mechanisms*. These mechanisms have evolved to cope with recurrent situations in the ancestral environment (e.g., Crawford 1998). Whenever an individual is confronted with a cue signaling such a situation, the mechanism is

triggered and the appropriate responses become salient (Tooby and Cosmides 1990b). An important role is played by emotions, coordinated systems of internal mechanisms, functioning as to link the ancestrally appropriate behavioral response to a specific adaptive problem (Cosmides and Tooby 2000; Plutchik 1980). For example, the cue "large fanged animal" activates the emotion of fear, which prepares the organism for the appropriate response: to flee.

One of these internal mechanisms is concerned with assigning priorities in case of different, and competing, cues from the environment (Cosmides and Tooby 2000; Tooby and Cosmides 1990b). For example, one might be simultaneously confronted with an attractive member of the opposite sex who is willing to mate, and with a predator. Depending on the relative importance of both cues, the prioritizing mechanism decides which behavioral response is activated.

Within evolutionary psychology, much attention has been devoted to the formulation of ancestrally evolved mechanisms that correspond highly with either of the relational models discussed above. In contrast, the question of which of these mechanisms has priority has received only little attention. In the remainder of this section, we first discuss the literature on either mechanism, starting with the mechanism corresponding to exchange behavior, and ending with the mechanism corresponding to communal behavior. Next, the matter of priority is raised, more specific, we address the question what happens when a person is confronted with a situation in which both cues for the mechanism for communal behavior and the mechanism for exchange behavior are present.

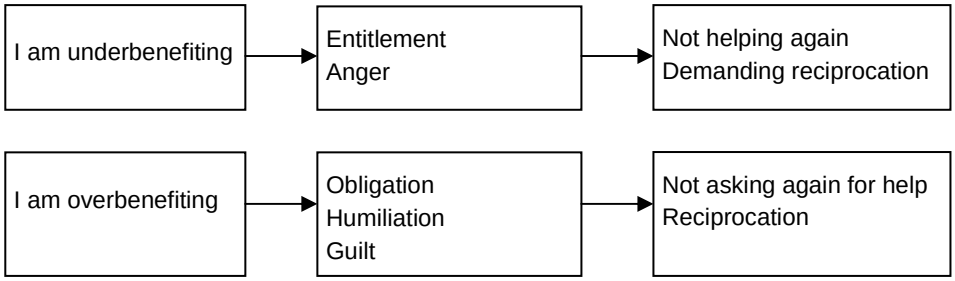
2.1 Exchange behavior or scorekeeping

The evolutionary psychological translation for exchange behavior would be *reciprocal altruism*, which is defined as providing benefits to another individual, at a cost to one's own fitness, which are returned in the future (Trivers 1971). Individuals who unconditionally provide benefits to others are vulnerable to exploitation by those who reap the benefits of other's helping behavior, without providing benefits in return. Therefore, it is argued, we are equipped with a mechanism which makes helping behavior *contingent* on the helping behavior of the other. The idea is that individuals keep track of the benefits received and provided, and only provide benefits to another individual if this does not result in a disadvantageous misbalance of books (Brown 1983; Dugatkin 1997; McElreath et al. 2003).

The central cue of such a scorekeeping mechanism is the balance in benefits received and benefits provided: if the relationship is imbalanced and I am

in an underbenefiting position, this triggers emotions of entitlement or even anger, leading to behavior aimed at recovering the balance between benefits provided and received. On the other hand, the reversed situation might be harmful too. To avoid that an interaction partner will consider me an exploiter, I have to avoid overbenefiting too. Thus, if I am in an overbenefiting position, this triggers emotions of obligation, humiliation and guilt, resulting in behavior aimed at recovering balance (Nesse 1991; Parker 1998; Trivers 1971). See Figure 4.1.

Figure 4.1: Scorekeeping mechanisms (avoiding underbenefiting and avoiding overbenefiting)



The most extensive elaboration of a scorekeeping mechanism is Cosmides and Tooby's mechanism for cheater detection (Cosmides 1989; Cosmides and Tooby 1992). Focusing on the need to avoid exploitation, they propose that humans are very sensitive to situations in which a person accepts benefits without giving anything in return. Empirical support for such a mechanism for cheater detection comes from experiments demonstrating that subjects are much better at detecting violations of logical arguments involving the violation of a social contract than those involving violations of descriptive conjectures (see also Gigerenzer and Hug 1992).

In addition to the results of cheater detection experiments, there are also results from other fields supporting the idea of a mechanism for avoiding disadvantageous misbalances. First, game theoretical studies have demonstrated the success of conditionally cooperative strategies, such as Tit-for-Tat (Axelrod 1984). Moreover, exchange experiments have shown that real subjects do indeed match the benefits they provide to the benefits provided by their interaction partner (e.g., Galluci and Perugini 2000; Pruitt 1968). Support for avoidance of advantageous misbalances, or overbenefiting, is provided by studies in the field of equity theory

(Walster et al. 1978). Experiments and questionnaire studies have shown that people avoid to ask others for help if they are not able to pay them back (e.g., Greenberg and Shapiro 1971), are more motivated to offer help to a person if this person has helped before (e.g., Greenberg and Bar-Tal 1976; Gross and Latané 1974), and experience negative emotions after overbenefiting (e.g., Castro 1974; Buunk et al. 1993). Finally, the results of experiments with ultimatum bargaining and dictator games provide evidence that people have a strong aversion to both overbenefiting and underbenefiting. Thus, subjects tend to divide rewards equally, even if they cannot be punished by the receiver, and tend to reject unfair offers, preferring to receive no reward to an unfair reward (Forsythe et al. 1994; Henrich et al. 2001; Kahneman et al. 1987).

2.2 Communal behavior or bonding

Communal behavior has received less attention than exchange behavior within evolutionary psychology. However, a number of studies stress the importance of relational cohesion (Lawler and Yoon 1996), commitment (De Vos et al. 2001), a need for deeply engaged friends (Tooby and Cosmides 1996), a need to belong (Baumeister and Leary 1995; Caporael et al. 1989), or a group heuristic (Yamagishi et al. 1999).

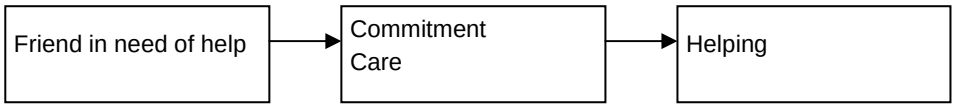
The basic idea of these studies is that the Pleistocene savanna exerted selection pressures for social group living. Food resources were patchily distributed, making an individual's foraging success unpredictable (Foley 1987; Kurland and Beckerman 1985). Furthermore, single individuals were more vulnerable to predator attacks. Individuals endowed with mechanisms that supported the maintenance of group membership were better off than individuals who were not (Baumeister and Leary 1995; Caporael et al. 1989). Such a mechanism would not only produce feelings of attachment towards one's group members, leading one to linger with the group, and thus to *receive* the benefits of protection and food sharing, but also feelings of commitment and care, resulting in the *providing* of benefits to one's group members. In the savanna environment, ignoring a person's need for help might have resulted in the loss of a valuable group member (De Vos et al. 2001; Tooby and Cosmides 1996). In sum, the high level of interdependence forced individuals not only to reap the benefits of group membership, but also to care for the survival and well-being of one's group members.

We use the term *bonding mechanism* to denote the mechanism responsible for this behavior. The central cues for such a mechanism are both the *need* of the

other person and the *relationship with the other*. If confronted with a person who was part of one's group and who was in need of help, individuals would respond with helping behavior, even if this resulted in an imbalanced relationship. This does not imply, however, that on the long term, relationships would not be balanced. In contrast, since even the best hunter had a fair chance of failing in capturing game, responding to each other's needs would have resulted in everyone helping each other approximately equally often. The difference with the scorekeeping mechanism is that one's helping behavior is dependent on the other's need rather than the difference between benefits provided and benefits received.

In the ancestral environment, individuals spent most of their lives in the same group. It is plausible therefore, that *every group member* triggered the emotions of commitment and care, and the appropriate bonding behavior, when in need. In the present environment, group membership is not so clear anymore. The most appropriate translation of "one's group" would be the circle of one's closest affiliates, that is, one's friends and family. If one of these persons is in need, emotions of commitment and care will be triggered, resulting in a willingness to provide help, regardless of possible imbalances. See Figure 4.2.

Figure 4.2: Bonding mechanism



Support for the claim that group membership is still a highly salient goal for humans comes from numerous experiments in the field of social identity theory (Tajfel 1981). Triggering the feeling of being part of a group in experimental subjects has proved to be very easy, requiring only the perception of being similar (for example preferring Kandinsky to Klee) or interdependent (for example receiving the same rewards) (see for a review Yamagishi et al. 1999). Moreover, exchange experiments have shown that after interacting repeatedly and successfully, subjects experience feelings of commitment towards their exchange partners, and consider their relationship as a valued object in itself (Kollock 1994; Lawler and Yoon 1996). In addition to support for the salience of group membership, social identity studies also provide support to the idea that group membership leads individuals to behave cooperatively towards people from their

group. After being exposed to a group identity trigger, subjects favor ingroup members as opposed to outgroup members when allocating rewards (Tajfel et al 197) and they contribute more to a public good (Brewer and Kramer 1986).

Furthermore, numerous studies in the field of social support theory have emphasized the importance of friendship for an individual's emotional and physical well-being (see for references Stroebe and Stroebe 1996; Uchino et al. 1996). Being part of a social support network reduces stress and increases life satisfaction, even in the absence of explicit emotional or practical assistance (Rook 1987; Cohen and Wills 1985).

Support for the importance of friendship in situations concerning the providing of benefits is manifold. The observation that friendship does not fit the traditional model of self-interested individuals was precisely the reason to introduce the distinction between communal and exchange relationships. In addition to the studies already mentioned in the Section 1, there are many other studies demonstrating that friends help each other because they care for the other rather than out of scorekeeping considerations. First, although equity theory provides support to the importance of scorekeeping considerations, the results of some studies suggest that the predictions of equity theory do not hold *in all relationships*. If the other person is a friend, the avoidance of both underbenefiting and overbenefiting plays much less a role than if the other person is a stranger (e.g., Morgan and Sawyer 1979). The issue of whether equity considerations vary according to relationship type is controversial, however. Social exchange theorists maintain that also close relationships are governed by exchange principles (Burgess and Huston 1979; Altman and Taylor 1973). Furthermore, a number studies suggest that friendships that are equitable are considered more satisfactory than friendships that are inequitable (e.g., Buunk and Prins 1998), and that subjects who like each other more are more aversive to inequity than subjects who like each other less (Clark et al. 1974). The second source of evidence for the contention that reciprocal altruistic behavior between friends is guided by the bonding mechanism rather than the scorekeeping mechanism comes from studies showing that non-comparability, or imbalance of benefits provided and benefits received, is associated with high friendship intensity (Clark 1981; O'Connell 1984). In a similar vein, Hays (1985) found friendship intensity to be more highly correlated with the benefits-plus-costs, accruing from the relationship, than with the benefits-minus-costs, suggesting that people positively value the making of sacrifices for friends. Third, in addition to being important to one's wellbeing, social support relationships are also characterized as being typically asymmetrical and unbalanced (Biegel and Naperstek 1982; Stewart 1989).

Finally, cultural anthropological studies on food sharing in hunter-gatherers stress motivations related to the bonding mechanism, that is: generousness, to help if there is a need, and the absence of an obligation to repay (Bird-David 1990; Harris 1980, p. 226-228; Wiessner,1996). Although evolutionary anthropologists have attempted to demonstrate that food sharing is guided by scorekeeping mechanisms (see for references Gurven, in press), the evidence is mostly restricted to correlations between giving and receiving. As a consequence, their results can be just as well explained by a bonding mechanism (Smaniotto, submitted).

2.3 Priorities and preparedness

Having argued that humans have two behavioral mechanisms that are triggered by different cues and produce different emotional and behavioral responses, the question rises what will happen if a situation contains cues for both mechanisms, triggering opposite behavioral responses. For example, what mechanism will be activated if I am asked for help by *a close friend who is in distress*, who is however *in my debt*? If I had only a scorekeeping mechanism I would refuse to help until he would have repaid his debts (see Section 2.1). In contrast, if I had only a bonding mechanism, I would provide help regardless of differences in benefits provided and benefits received (see Section 2.2). In the presence of two competing cues, triggering opposite behavioral responses, *what* response will be actually given depends on which of the two cues has priority.

Most evolutionary psychological studies related to scorekeeping or bonding, address one of either mechanisms in isolation. For example, in the social contract argument which is used in the cheater detection experiments, subjects are presented only with cues signaling an imbalance in benefits provided and benefits received, without reference to the relationship with the other person (Cosmides 1989; Cosmides and Tooby 1992; Gigerenzer and Hug 1996). Exceptions are formed by a number of theoretical treatments in which distinctions similar to those between communal and exchange relationships are provided with an evolutionary psychological background (see for example, Bugenthal 2000). The question what will happen when the relationship has both characteristics of an exchange relationship and a communal relationship is not addressed, however.

According to Tooby and Cosmides (1990b; Cosmides and Tooby 2000), emotion mechanisms consist not only of algorithms linking single cues to the appropriate cognitive, emotional and behavioral responses, but also of algorithms prescribing which cue has priority in case of two competing cues. The question of

how such priority assigning algorithms should be envisioned has received little attention, however. One possibility is to think of them in terms of *biological preparedness* (Cummins 2001). Originally introduced to eliminate the dichotomy of innateness versus learning as portrayed in the nature-nurture debate, this term links the criticalness of an adaptive problem in the ancestral environment with the ability of the newborn mind to very quickly develop and learn specialized cognitive, emotional and behavioral functions (Cummins and Cummins 1999). Put more simply: responses that were highly important to our ancestors' survival are easier to learn than responses that were less important. Examples of such easily acquired responses are fear responses towards certain classes of animals (spiders and snakes) (Öhmann and Dimberg 1978; Seligman 1971), as well as taste aversions to foods that make one ill (Garcia, Brett and Rusiniak 1989). It seems plausible that this preparedness of responses that were critical for our ancestors' survival is not only expressed by the ease which they are learnt, but also by the ease with which the responsible mechanisms are *activated* – or, in other words, by the priority assigned to the cue.

Which of the two mechanisms described above has priority? We address this issue using a similar argument as was presented by Tooby and Cosmides (1996) in their article on the Banker's Paradox, that is, the problem that persons who are in most dire need are also the worst credit risks, and consequently, are least attractive as recipients of assistance. In this article, they make a similar distinction as the one between exchange and communal relationships, namely between the *exchange domain* and the *friendship domain*, arguing that "*the altruistic adaptations that underlie friendships do not map onto the structure of tit for tat or any other standard models of reciprocal altruism based on alternating sequences of contingent behaviors*." (p. 131). Friendship relations are characterized by a spontaneous pleasure to help the other, without looking for a contingent return. Exchange relations, on the other hand, are characterized by explicit contingent exchange and turn-taking reciprocation (p. 139; see also Silk 2003). The solution to the banker's paradox is to cultivate relationships with those people who are committed to you, that is, to cultivate friendships. By becoming irreplaceable for a number of others, you will be assured of help when you are in distress: the consideration that you might not repay your debt is overruled by the consideration that you are too valuable to lose.

The argument applies exceptionally well to the ancestral environment, in which the survival of one's group members was a precondition for one's own survival. In those conditions, the possible consequences of ignoring a group member in need were much more serious than the threat of being cheated. Therefore it can be expected that in the presence of the competing cues, *friend in*

distress and an *imbalance in benefits provided and benefits received*, the first cue has a higher priority and the bonding mechanism is more easily triggered than the scorekeeping mechanism. This results in helping the needy friend rather than trying to maintain a balanced relationship.

2.4 Hypotheses

In order to test the hypothesis that in case of conflicting cues, the bonding cues have a higher priority than the scorekeeping cues, we have to consider situations in which both competing cues are present. The scorekeeping cues boil down to some imbalance in benefits received and benefits provided, and the bonding cues boil down to a need for help on the part of a *friend*. Therefore, we expect individuals confronted with a dilemma between helping someone in need and restoring balance between benefits received and benefits provided, will be more likely to provide help if the other is a *friend* than if the other is an *acquaintance* (H1).

Furthermore, we can also expect an effect of the context of the helping situation. We will consider two objects of help, one the typical commodity of modern market society: money; the other a timeless commodity: the providing of help in the case of illness. We expect individuals confronted with the dilemma between helping someone in need and restoring the balance between benefits received, to be more likely to choose the option of helping if the other person is ill than if the other person is out of money. Thus, the degree of bonding responses is expected to be higher in the illness context than in the money context. One reason is that the illness context is more resembling to ancestral helping situations, and therefore will activate the ancestrally relevant behavioral mechanisms to a higher degree (Kanazawa 2003). In addition, since being ill, in contrast to being without money, is potentially life-threatening, it is generally considered to constitute a greater need than being in need of money. Since bonding behavior is limited to the people in one's closest circle, the increase in helping behavior in the illness context should be stronger for friends than for acquaintances (H2).

The third hypothesis is directed at testing the difference in priority between the bonding and the scorekeeping most explicitly. Since losing an interaction partner was more detrimental to a person's survival than being cheated in the ancestral environment, the bonding mechanism should have priority over the scorekeeping mechanism. As was argued before, a plausible way to study differences in priority between two behavioral mechanisms is by focusing on the difference in the ease with which they are triggered. Thus, it can be expected that a very subtle, or *implicit* prime for either scorekeeping or bonding behavior, has a

stronger impact on the bonding mechanism than the scorekeeping mechanism. Thus, the increase in bonding responses after exposure to an implicit bonding prime should be larger than the increase in scorekeeping responses after exposure to an implicit scorekeeping prime (H3).

3 Methods

3.1 Scenarios

The hypotheses were tested using a scenario design. The scenarios described dilemma situations with one or two others. Each situation contained cues for both the scorekeeping mechanism and the bonding mechanism. Using semantic differential scales, subjects were asked how they would feel and how they would behave in such a situation. Behavioral response was measured on a four-point scale, designed in such a way that the answering categories indicated a *definite scorekeeping response*, a *probable scorekeeping response,* a *probable bonding response*, and a *definite bonding response*. Three scenarios were used (see Figure 4.3), two of them posing a dilemma between helping someone who is in need and avoiding underbenefiting (*Debtor in need* and *Refuser in need dilemma*) and one posing a dilemma between helping someone who is in need and avoiding overbenefiting (*Reciprocate vs help dilemma*). The complete scenarios are presented in Appendix 1.

The scenarios concerning the dilemma between avoiding underbenefiting and helping a needy one, both involve one actor who is in need and who requests for help. In the *Debtor in need dilemma*, the requester is someone who already received help from the subject recently. Helping him again would imply an increase in the imbalance of benefits received and benefits provided, and put the subject at risk of being cheated. By refusing to help, one would stop him from getting indebted any further. Thus, granting the request is the typical bonding response, whereas refusing to help is the typical scorekeeping response. The *Refuser in need dilemma* was included as a more literal translation of the tit for tat strategy. It is similar to the *Debtor in need dilemma*, except that the requester is someone who has recently refused to grant a request for help on the subject's part. Again, helping this person would put a subject at risk of being cheated. By refusing to help they would retaliate his previous behavior. To emphasize the seriousness of the actors' need for help, in both the *Debtor in need* and the *Refuser in need dilemma*, subjects were informed that the actors did not know many people whom they could appeal to. Behavioral response was measured on a four-point scale, with answering categories

definitely not helping, probably not helping, probably helping, and definitely helping.

In contrast to the dilemma between avoiding underbenefiting and helping a needy one, it is impossible to devise a dilemma between avoiding overbenefiting and helping a needy one if only one actor is involved. If a person from whom I am overbenefiting is in need, both the bonding and the scorekeeping mechanism would respond with providing help. Therefore, a scenario involving two actors was devised, where the dilemma consists of which actor to provide benefits to. In this scenario, both actors request for help at the same time. The first actor (A.) is only mildly in need, whereas the second actor (S.) is highly in need. However, A. recently granted a similar request for help by the subject. Thus, if the subject chooses to repay A., he attaches higher priority to avoiding overbenefiting. A choice for helping S. indicates a preference for helping those who are in need. Again, a four-point scale was used, with answering categories definitely repaying A., probably repaying A., probably helping S., and definitely helping S. Subjects were informed that they did not have enough resources to provide benefits to both actors, that they had known both actors for about an equally long period, that A. and S. earned about the same income, and that they did not know many persons whom they could appeal to.

Figure 4.3: Overview of the three dilemma situations

Name of dilemma	Scorekeeping cue (see Fig 4.1)	Bonding cue (see Fig 4.2) #	Scorekeeping response (see Fig 4.1)	Bonding response (see Fig 4.2) #
Reciprocate vs help dilemma	I am indebted to $Alter_1$.	$Alter_1$ is mildly in need $Alter_2$ is highly in need	Reciprocate $Alter_1$	Help $Alter_2$
Debtor in need dilemma	Alter is in my debt	Alter is in need	Not help Alter	Help Alter
Refuser in need dilemma	Alter has refused to help me.	Alter is in need	Not help Alter	Help Alter

Based on our *hypotheses* the bonding mechanism should be more highly activated if Alter is a friend. In order to test this hypothesis, the *experimental design* should allow both friends and acquaintances to get in need.

3.2 Experimental conditions

To determine the effects of Relationship with Alter, Context and Prime, a 2 by 2 by 3 factorial design was used. Relationship with Alter was varied by giving half of the subjects dilemma situations in which Alter was designated as "friend", and half of the subjects dilemma situations in which Alter was designated as "acquaintance".

Context was varied between a money context and an illness context: half of the subjects received dilemma situations in which the object of help was providing assistance in the case of illness, and half of the subjects received dilemma situations in which the object of help was lending money. In the money context, the request for help involved a request to borrow 100 euros, either because the actor's purse had been stolen (in the *Help debtor* and *Help refuser dilemma* and in case of the needy one (S.) in the *Reciprocate vs help dilemma*) or because the actor wanted to buy new clothes (in case of the creditor (A.) in the *Reciprocate vs help dilemma*). In the illness context, the request involved coming over to the ill person's house the next day in order to nurse him. In the *Reciprocate vs help dilemma*, the mild need was operationalized by A. having caught a touch of flu, whereas S.' illness was described as more serious, preventing him from leaving the house.

Finally, Prime was varied between a bonding prime, a scorekeeping prime and a neutral prime. This was done by giving one third of the subjects a task in which they had to read a story about a typical bonding situation, one third a story about a typical scorekeeping situation, and one third a "neutral" story. Since this condition was only present in *Study 2*, we will discuss it in more detail when discussing that study.

4 Study 1

4.1 Method

Participants

To test the hypotheses concerning Relationship with Alter and Context, a large group of first-year business students and a smaller group of first-year sociology students were asked to fill out a 5-minutes-questionnaire. On both occasions, questionnaires were handed out during a lecture. From the business students 355 questionnaires were returned, and from the sociologists 38. After discarding questionnaires that were not completed or that did not appear to be completed in a serious manner, a number of 346 remained, 313 of which belonged to business

students and 33 of which belonged to sociology students. Of this number, 63% concerned men and 37% concerned women. The average age was 19 years (sd=2).

Design

The questionnaire consisted of three descriptions of situations about reciprocal altruistic behavior between the subject and one or two others. The primary goal of this questionnaire was establishing a correlation between emotional response and behavior, so only one of the scenarios, the *Reciprocate vs help dilemma,* was used for this study. Both *Relationship with Alter* and *Context* were varied between subjects.

4.2 Results

From the 346 valid cases 21.1% responded that he/she would definitely pay back A; 26.0% would probably pay back A; 31.8% would probably help S and 21.1% would definitely help S. The overall mean on the variable - which ranged from 1 tot 4, with 1 signifying a definite scorekeeping response, and 4 signifying a definite bonding response - was 2.53 (sd=1.05).

In order to test the hypotheses while controlling for all variables, an ANOVA was conducted with behavioral response as dependent variable and Context and Relationship with Alter as independent variables. In addition, Sex and Study were included as control variables. There was only a significant effect of Context [$F(1,330)=5.69$; $p<0.05$]: subjects in the illness condition scored significantly higher on bonding than subjects in the money condition (2.84 and 2.21, respectively). There were no significant main effects of Relationship with Alter [$F(1,330)= 1.26$]; Study [$F(1,330)=2.82$], or Sex [$F(1,330)=0.44$], nor any interaction effects (see Table 4.1).

In conclusion, the results suggest that one's decision to help a needy person, rather than repay a creditor is significantly influenced by the object of help. If the object of help is providing assistance in the case of illness, subjects are more likely to provide help than if the object of help is money. Relationship with Alter has no significant effect, neither as a main effect, nor as an interaction effect with Context. The results might be the consequence of the Reciprocate vs help dilemma being an atypical dilemma situation, since it involves the dilemma between helping and avoiding to be in another person's debt. Since Study 2 includes both the same dilemma situation as in Study 1, as well as two other dilemma situations, it can be checked whether these results are replicated, and whether scenarios involving the dilemma between helping and avoiding underbenefiting yield different results.

Table 4.1: Mean behavioral response, sd, and N according to experimental condition (Study 1)

Context	Relationship with Alter	M	sd	N
Illness	Friend	2.82	0.98	87
	Acquaintance	2.85	1.02	89
	Total	2.84	1.00	176
Money	Friend	2.16	0.96	88
	Acquaintance	2.27	1.06	82
	Total	2.21	1.00	170
Total	Friend	2.49	1.02	175
	Acquaintance	2.57	1.07	171
	All	2.53	1.05	346

Note: Behavioral response was measured on a 4-point scale, with 1=definitely scorekeeping and 4=definitely bonding.

5 Study 2

5.1 Method

Participants

Respondents in *Study 2* consisted of 402 first-year psychology students, who had to spend three half days filling out questionnaires as part of their curriculum. The relevant questionnaire was scheduled halfway through the first day. Completing it took about 15 minutes. After discarding the questionnaires that were incomplete, 353 remained. Of this number 25.5% concerned men and 74.5% concerned women. The average age was 20 years (sd=4).

Design

As in *Study 1*, Context and Relationship with Alter were manipulated. In addition to these manipulations, subjects were administered an implicit prime for either bonding behavior or scorekeeping behavior. A third group received a neutral prime. The prime was administered through a bogus language test. Subjects had to correct the spelling in a short text, which was introduced as written by a student. The texts concerned an experience of doing an assignment for a university course. In all three conditions the student only marginally passed because of a problem

with his co-worker (in the bonding prime and scorekeeping prime conditions) or with his computer (in the neutral prime condition). In the bonding prime condition, the writer had to work with another student who appeared to have a serious illness, and the writer decided to help the student at the expense of his own mark, because "that is what friends are supposed to do". In the scorekeeping prime condition, the writer had to work with another student who appeared to be a freerider, and the writer decided to dash off his part of the assignment too, because "being taken advantage of is one of the most frustrating things in life". In the neutral prime condition, the student had to work on an individual assignment and got into problems when his computer crashed.

After finishing the test, subjects continued with the second part of the questionnaire, which consisted of the three dilemma situations discussed above. In order to avoid order effects, the order of the three dilemmas was randomly varied between questionnaires.

5.2 Results

In *Study 2*, three dilemma situations were used to measure subjects' behavioral responses when confronted with a situation containing both scorekeeping and bonding cues. To analyse the data, an ANOVA with Repeated Measures was performed. The responses on the three dilemma situations were treated as a within-subjects variable with 3 levels (called "Dilemma"). To determine whether it is justified to consider the three dilemmas as repeated measures of the same variable, we start with presenting some descriptives and correlations.

5.2.1 Description of data

Table 4.2 shows the distribution of responses on the three dilemmas. The *Debtor in need dilemma* evokes the largest degree of bonding responses. Of all respondents, 74.5% choose a probable or definite bonding response. Although not so overwhelming, the *Reciprocate vs help* and the *Refuser in need dilemma* also evoke a majority of bonding responses (percentage of bonding responses is 61.5% and 57.5% respectively).

Table 4.2: Distribution of responses on the three dilemmas

		Reciprocate vs help	Debtor in need	Refuser in need
Definitely scorekeeping	(1)	14.4 %	4.5 %	10.2 %
Probably scorekeeping	(2)	24.1 %	21.0 %	32.3 %
Probably bonding	(3)	46.2 %	45.6 %	49.3 %
Definitely bonding	(4)	15.3 %	28.9 %	8.2 %
Mean		2.62	2.99	2.56
Sd		.91	.83	.79
N		353	353	353

Note: Only subjects who responded to all scenarios are included.

If the three dilemmas measure the same variable, as was assumed, a minimal requirement would be that they are positively correlated. Correlations are 0.42 for the *Reciprocate vs help* and *Debtor in need dilemma*, 0.16 for the *Reciprocate vs help* and *Refuser in need dilemma* and 0.33 for the *Debtor in need* and *Refuser in need dilemma* (all correlations are significant at $p<0.01$; 1-tailed tests). Although not all correlations are equally strong, it seems justified to consider the three dilemmas as measuring the same underlying variable.

5.2.2 Repeated Measures ANOVA

To test the hypotheses, an ANOVA with Repeated Measures was performed. Behavioral responses to the three dilemma situations was treated as a within-subjects factor with thee levels. Context, Relationship with Alter, Prime and Sex were included as independent variables. Sex did not have a main effect [$F(1,321)=.263$], nor any interaction effects, so it was excluded. (See Appendix 2 for the mean behavioral responses in all conditions)

Between-subjects analyses showed significant main effects of all independent variables, Context [$F(1,341)=220.7$; $p<0.01$]; Relationship with Alter [$F(1,341)=6.3$; $p<0.05$] and Prime [$F(2,341)=4.2$; $p<0.05$]. In addition, there was a 3-way interaction effect of Prime, Context and Relationship with Alter [$F(2,341)=4.8$; $p<0.01$].

Moreover, a number of within-subjects effects (Multivariate tests) were found, indicating differences in behavioral responses between the three dilemmas. These effects concerned a main effect of Dilemma [$F(2,340)=51.8$; $p<0.01$], a 2-way interaction effect of Dilemma and Context [$F(2,340)=17.8$; $p<0.01$] and a 3-way interaction effect of Dilemma, Context and Relationship with Alter [$F(2,340)=3.1$; $p<0.05$]. To interpret the within-subjects effects, three additional Univariate ANOVA's were conducted, with subsequently, responses on the *Reciprocate vs help dilemma*, *Debtor in need dilemma* and *Refuser in need dilemma* as dependent variables.

In the following, the effects of Relationship with Alter, Context and Prime are discussed. Next, the remaining significant effects of the Repeated Measures ANOVA are considered. Where necessary, the results of the Univariate ANOVA's are reported.

Effect of Relationship with Alter

The difference between responses towards friends and responses towards acquaintances is small but significant. The estimated mean response on the compound variable Dilemma is 2.78 towards friends and 2.65 towards acquaintances. Thus, towards friends subjects are slightly more likely to behave according to the bonding mechanism than towards acquaintances. The results of three additional Univariate ANOVA's show that the *Refuser in need dilemma* holds the strongest effect of Relationship with Alter [$F(1,367)=10.0$; $p<0.01$] (see Figure 4.4). In the *Reciprocate vs help* and *Debtor in need dilemma* the effect of Relationship with Alter is in the expected direction, but in neither of them does it reach significance [$F(1,361)=0.01$ and $F(1,369)=1.86$, respectively].

The weak effect of Relationship with Alter might have been the result of the used operationalization. The bonding mechanism was theorized to be triggered by a person *who is part of my closest circle*, being in need of help. Using *"friend"* as *a person who is part of my closest circle* seems to be an obvious operationalization. To use "*acquaintance"* as *a person who is NOT part of my closest circle* is less obvious. The intuitive alternative "stranger" is problematic since strangers are, by definition, not in one's debt. As a consequence this operationalization, the degree of bonding responses in the acquaintance condition might have been overestimated. Likely, some people consider their acquaintances to be part of their closest circle too. Thus, in an unpublished study in which Context and Relationship with Alter were manipulated, a number of subjects in the acquaintance condition complained that "acquaintance" was too vague a concept. Moreover, several subjects explicitly

mentioned that they had interpreted "acquaintance" as "friend". Therefore, a different operationalization of the theoretical concept *a person who is not part of my closest circle* might have resulted in a lower amount of bonding responses in the acquaintance condition and a more pronounced effect of Relationship with Alter.

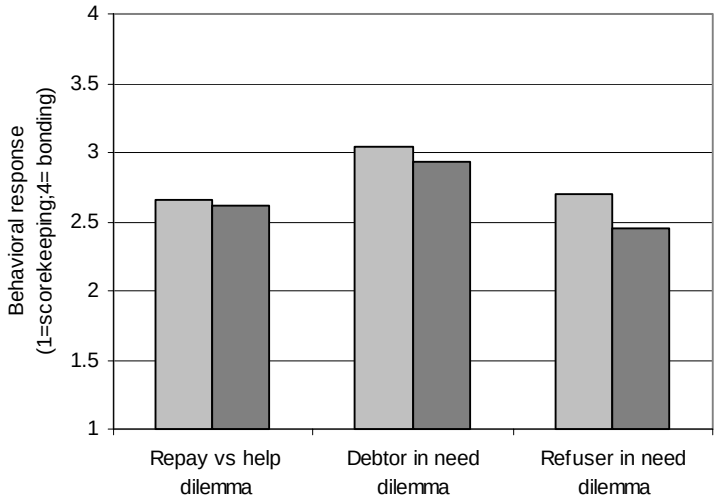


Figure 4.4: Effect of Relationship with Alter in the different dilemmas

Effect of Context

The context of the situation has by far the largest effect on subjects' responses. In the money context, the estimated mean response on the compound variable Dilemma is 2.34; in the illness context it is 3.09. Univariate analyses show that the effect of Context is significant in all three dilemmas (*Reciprocate vs help dilemma:* $F(1,361)= 106.4$; $p<0.01$, *Debtor in need dilemma:* $F(1,369)=194.6$; $p<0.01$, *Refuser in need dilemma:* $F(1,367)= 25.7$; $p<0.01$) (see Figure 4.5).

In contrast to our expectations the effect of Context is not larger in the friend condition than in the acquaintance condition: there is no significant 2-way interaction effect of Relationship with Alter and Context [$F(1,341)=.04$]. Thus, subjects are more likely to help someone in need rather than keep the books balanced if the object of help concerns assistance in the case of illness than if it

concerns money, and the increase in bonding responses is present towards both friends and acquaintances.

Although there is no 2-way interaction effect of Context and Relationship, there is a significant 3-way interaction effect of Dilemma, Context and Relationship with Alter. Figures 4.6a and 4.6b show that this interaction effect is mainly due to the *Debtor in need dilemma*, where there is a difference between friends and acquaintances with regard to the degree of bonding responses in the money context (Figure 4.6a), but not in the illness context (Figure 4.6b). The presence of an interaction effect of Context and Relationship with Alter in the *Debtor in need dilemma* is confirmed by the Univariate ANOVA [$F(1,369)=4.58$; $p<0.05$]. In the other two dilemmas it is non-significant (*Reciprocate vs help dilemma*: $F(1,361)=.43$; *Refuser in need dilemma:* $F(1,367) =.44$)

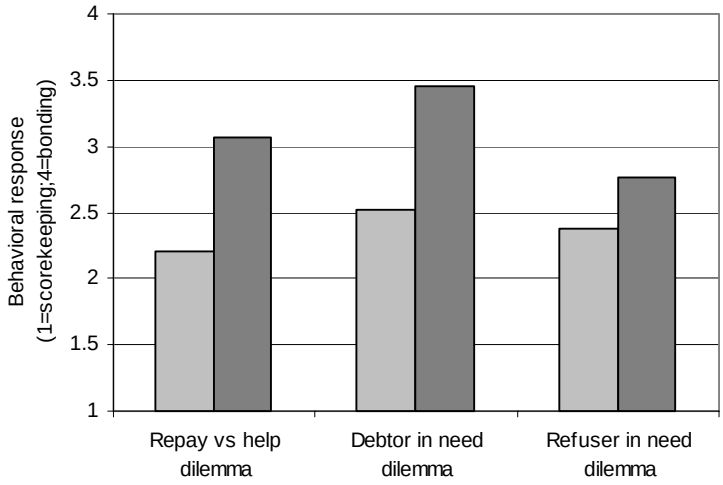


Figure 4.5: Effect of Context in the different dilemmas

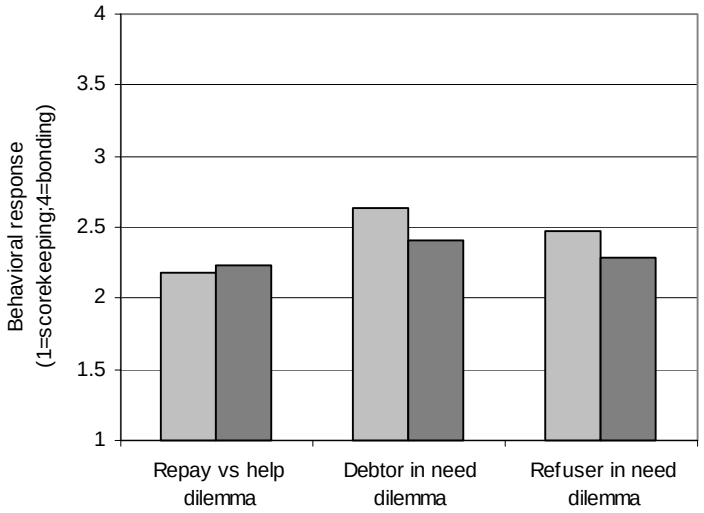


Figure 4.6a: Effect of Relationship with Alter in the different dilemmas: Money context

Key: Friend Acquaintance

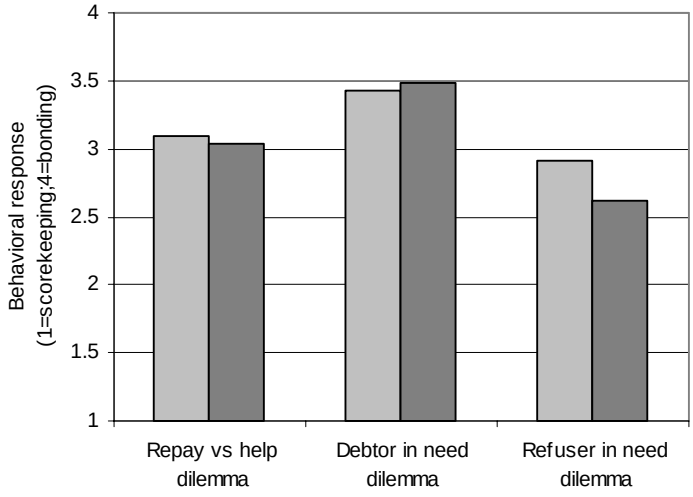


Figure 4.6b: Effect of Relationship with Alter in the different dilemmas: Illness context

Key: Friend Acquaintance

Apparently, subjects do not distinguish between friends and acquaintances who are in their debt if the object of help is assistance in the case of illness. In contrast, if the object of help is money, subjects are more likely to help the debtor if he is a friend than if he is an acquaintance. A possible explanation is that the illness context poses such a strong need cue that subjects are reluctant to ignore a person's request for help, even if he is just an acquaintance. The only case in which the illness context elicits a higher degree of help towards friends than towards acquaintances is in the dilemma with the lowest overall degree of bonding responses, the *Refuser in need dilemma* (see Figure 4.6b). This suggests that people are more lenient towards friends than towards acquaintances, and the more so if the other has refused to help at a previous encounter. This result contradicts the idea that being cheated by a friend evokes stronger negative reactions than being cheated by someone you do not know so well (McElraeth et al. 2003, p. 148). In the *Reciprocate vs help dilemma*, finally, the only effect comes from Context. This in accordance with the absence of any effect of Relationship with Alter in the *Reciprocate vs help dilemma* as appeared from *Study 1*.

Effect of prime

The implicit prime has a small but significant main effect. However, the direction is unexpected: pairwise comparisons show that the estimated mean responses on the compound variable do not differ significantly if comparing the bonding prime and the scorekeeping prime (M=2.67; SE=0.04 and M=2.66; SE=0.05, respectively). Comparing the mean response in the neutral prime condition (M=2.82; SE=0.04) with the two other conditions shows that both differences are significant (both comparisons $p<0.05$). Thus, whereas subjects in the bonding and scorekeeping prime conditions do not differ in their response, subjects in the neutral condition respond more in a bonding way. This result is hard to interpret, since it contradicts both the hypothesis formulated in this study (the bonding prime has a stronger effect than the scorekeeping prime), *and* the alternative hypothesis (the scorekeeping prime has a stronger effect than the bonding prime), *and* the nullhypothesis (no difference between prime conditions). Therefore, it seems that the prime manipulation has failed.

However, in addition to the main effect of Prime there is also a 3-way interaction effect of Prime, Context and Relationship with Alter, which is depicted in Figures 4.7a and 4.7b.

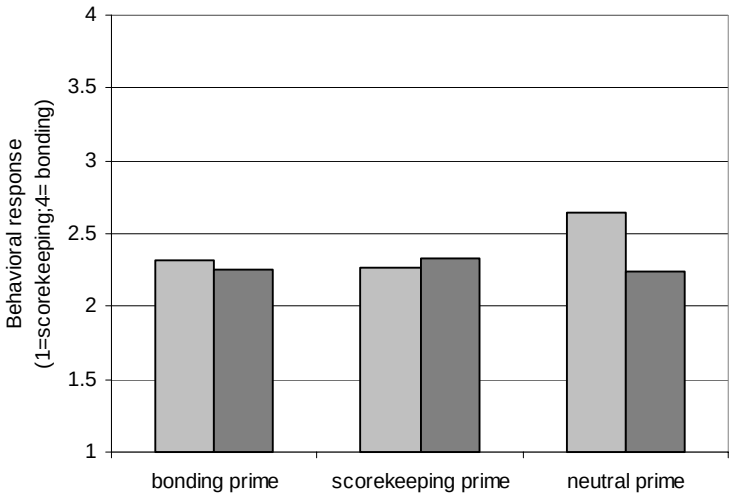


Figure 4.7a: Effect of Relationship with Alter according to Prime condition: Money context

Key: friend acquaintance

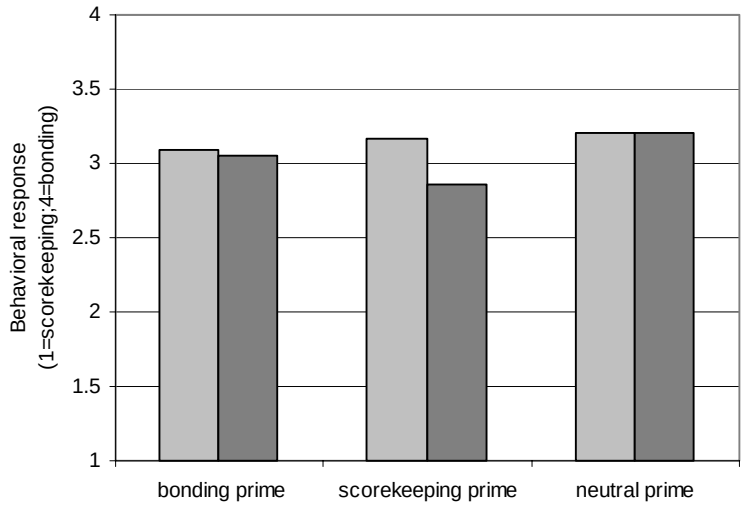


Figure 4.7b: Effect of Relationship with Alter according to Prime condition: Illness context

Key: friend acquaintance

The effect of Prime seems to be restricted to two conditions. First, in the *money context,* behavior towards *friends* is more bonding-oriented after receiving the *neutral prime*, than after receiving the bonding or the scorekeeping prime (pairwise comparisons of those specific conditions show that the neutral-bonding prime difference and the neutral-scorekeeping prime are significant at $p<0.05$ and $p<0.01$, respectively). Behavior towards acquaintances in the money context does not differ according to prime condition (Figure 4.7a). Second, in the *illness context*, subjects who have received the *scorekeeping prime*, respond with a lower degree of bonding responses than subjects presented with the neutral prime ($p<0.01$) (the difference with the bonding prime is non-significant), but only towards *acquaintances* (Figure 4.7b).

This last result suggests that – contrary to the expectations – the scorekeeping mechanism is triggered more easily than the bonding mechanism, but only if Alter is an acquaintance and in the illness context. The observation that the effect only occurs towards *acquaintances*, and not towards friends, suggests that scorekeeping is mainly directed at acquaintances. Although this result does not agree with our depiction of the two mechanisms and their relevant cues - Relationship with Alter was explicitly expected to be only a cue for the bonding mechanism - it does provide support to the key importance of one's relationship with the other person.

To find out whether any of these results are due to a fading effect of Prime after the first dilemma situation, we considered only the dilemma situation which came first in the questionnaire. Next, separate Univariate ANOVA's on behavioral responses to the *Reciprocate vs help, Debtor in need, and Refuser in need dilemma* were conducted. The results did not yield any support to such a "fading away" effect.

Other effects

The within-subjects analyses show a considerable effect of *Dilemma*, suggesting that the different dilemma situations give rise to different degree of bonding and scorekeeping responses. The same conclusion could already been drawn from the descriptive analyses (Section 5.2.1, Table 2), which showed that the *Debtor in need dilemma* evokes a higher degree of bonding response than the other two dilemmas.

As shown by the within-subjects analyses, there is an interaction effect of *Dilemma and Context* (see Figure 4.5). Two observations can be made that probably account for the interaction effect. First, the size of the effect of Context is considerably smaller in the *Refuser in need dilemma*, and second, the differences

between the three dilemmas are much larger in the illness context than in the money context. A possible explanation for these observations is that, confronted with an ill person, considerations concerning the balance in benefits provided and benefits received play a minor role. The person in need cannot be blamed for being ill two times in a row, which explains the extremely large degree of bonding responses in the *Debtor in need dilemma*. The presence of a less ill requester, towards whom I am in an overbenefiting position, decreases the amount of bonding responses to a lower, but still relatively high level (see *Reciprocate vs help dilemma*). However, the most legitimate reason for not helping an ill person - as appears from the relatively low degree of bonding responses in the *Refuser in need dilemma* - is a blunt refusal to help me when I was ill. In contrast, in the money context, considerations concerning the balance in benefits provided and benefits received are much more important. Both the presence of a second requester to whom I am indebted, and the person being in my debt, strongly reduce the degree of bonding responses to about the same level as in the *Refuser in need dilemma.*

6 Discussion

The two reported studies examined responses in situations constituting a dilemma between helping a person in need and maintaining a balance in benefits provided and benefits received. Helping a person in need was considered as the behavioral response resulting from the bonding mechanism, which is triggered by the cue *friend in need of help*. Conversely, a refusal to help a person who is in one's debt or who has refused to help in the past (in *the Debtor in need* and *Refuser in need dilemma*), as well as the choice to repay one's debts rather than help a person highly in need (in the *Reciprocate vs help dilemma*) was supposed to be the result of the scorekeeping mechanism, which is triggered by an imbalance in the relationship. Since the bonding mechanism was assumed to be only triggered by persons in one's closest circle, the degree of bonding responses was expected to be higher among subjects who received dilemma situations involving friends than among subjects who received dilemma situations involving acquaintances. In addition, assuming that illness poses both a more timeless and a more urgent need for help as compared to a want of money, it was predicted that subjects presented with illness scenarios were more likely to give a bonding response than subjects presented with money scenarios. One of the two studies also included an implicit prime for either scorekeeping or bonding behavior. It was hypothesized that if the bonding mechanism has a higher priority than the scorekeeping mechanism, subjects

receiving the bonding prime should show a stronger increase in bonding responses, compared to the increase in scorekeeping responses by the subjects receiving a scorekeeping prime.

In the remainder of this section, we evaluate the results and raise some issues that deserve future research.

Context of the dilemma situation and relationship with Alter

The results provide support to the idea that different conditions trigger different mechanisms of reciprocal altruism. The illness context evoked a higher degree of bonding responses than the money context in all dilemma situations, although the difference was less strong in the *Refuser in need dilemma*. Whether the effect of Context is due to a perceived difference in need between the money and illness context, or to the fact that the illness context triggers the more ancient of the two mechanisms, cannot be determined. In addition, there was some support that friends evoke more bonding behavior than acquaintances. *Study 1* showed no difference between responses towards friends versus acquaintance, but *Study 2* did, although the difference was most prominent in the *Refuser in need dilemma*. In sum, based on the differential effects of relationship with Alter and the context of the situation, it seems that the bonding mechanism is primarily activated by the object of help being timeless and potentially life-threatening, and much less by the other being a friend.

As was already mentioned, however, the weak effect of Relationship with Alter might be the result of subjects considering acquaintances as part of their closest circle too. Another reason might be the difference in salience of the Relationship with Alter and the Context manipulation. Relationship with Alter was manipulated by using the term *friend* versus *acquaintance* at a restricted number of locations in the questionnaire – once in the instruction, and once in each dilemma situation. In contrast, Context was manipulated by varying the description of the dilemma situation, which boiled down to a considerable difference in the precise stories. A possible way to increase the salience of the relationship with one's interaction partner would be to use more explicit terms to describe the relationship. The relationship manipulation would liven up even more if subjects are instructed to take in mind a particular person, either someone whom they consider a good friend, or someone whom they don't know so well.

Implicit prime

The effect of the implicit prime is hard to interpret. There was no increase in bonding responses after the bonding prime, and consequently, there was no evidence that the increase in bonding responses after exposure to the bonding prime was larger than the decrease in bonding responses after exposure to the scorekeeping prime. In only one condition was there a decrease in bonding responses after exposure to the scorekeeping prime, namely in the illness context and towards acquaintances. Although one might interpret this result as support for the alternative hypothesis, that is, the scorekeeping mechanism being more easily triggered than the bonding mechanism, the evidence is very thin. Thus, it seems safer to conclude that the prime manipulation did not work. It is plausible that the effect of the prime manipulation has been canceled out by the explicit manipulations. In general, studies using implicit primes do not also include explicit manipulations (see for references Fazio 2001).

In sum, although implicit primes might be a fruitful way of testing hypotheses about differences in priority, the formulation and selection of adequate prime manipulations requires extensive preliminary studies.

Differences between dilemma situations

The results of this study were based on three dilemma situations, two concerning a dilemma between helping a needy one and avoiding underbenefiting (*Debtor in need* and *Refuser in need dilemma*) and one concerning a dilemma between helping a needy one and avoiding overbenefiting (*Reciprocate vs help dilemma*). Since all of them were presented as dilemmas between helping a needy one and avoiding an imbalanced relationship, we did not formulate hypotheses about differences between dilemmas. However, the results showed that there were several of differences, especially between the two scenarios posing a dilemma between helping a needy one and avoiding underbenefiting (i.e., the *Debtor in need* and *Refuser in need dilemmas)*. In both dilemmas, the degree of bonding responses was higher in the illness context, as compared to the money context, and it was also higher towards friends, as compared to acquaintances. However, there were a number of results suggesting that we may need to qualify what exactly constitutes *avoiding underbenefiting*.

First, the *Debtor in need dilemma* evoked the highest amount of bonding responses, whereas the *Refuser in need dilemma* evoked the lowest amount of bonding responses. Second, in the illness context, a request for help was granted by the far majority of subjects in the *Debtor in need dilemma*, whereas it was much smaller in the

Refuser in need dilemma. And third, the effect of Relationship with Alter was most prominent in the *Refuser in need dilemma*. All these results suggest that people are less tolerant towards refusers than towards debtors, the more so if it concerns an illness context. Results from a study including not only behavioral responses but also personality and emotion measures, support this interpretation (Smaniotto and Stokman, submitted). Compared to subjects who were less prosocial, subjects who were more prosocial were more likely to provide help to a refuser, but not more likely to help a debtor. Furthermore, a *Debtor in need* triggered higher degrees of emotions like commitment, warmth and obligation, and less negative emotions like anger than did a *Refuser in need*. We tend to interpret these results in terms of the importance of responding to each other's needs. Although people do not mind underbenefiting in the sense of another person being indebted to them, they do mind underbenefiting in the sense of *another person not responding to their needs*. When that happens, they are less likely to grant a request for help, experience more negative emotions, need to be relatively prosocial to grant the request, and need to have a relatively close relationship with the other person to grant the request.

Conclusion

Although the question of differences in priority between the bonding and the scorekeeping mechanism remains unanswered, the two studies reported here provide strong support that different conditions trigger different mechanisms of reciprocal altruism. The results are consistent with social psychological studies showing that persons behave differently, depending on whether they have or desire a communal versus an exchange relationship with the other person (Clark 1984; Clark and Mills 1979). In contrast, the results oppose the idea that reciprocal altruistic behavior is solely guided by the avoidance of being cheated, or scorekeeping.

CHAPTER 5

Reciprocal altruistic behavior and emotions
Scorekeeping versus bonding[1]

1 Reciprocal altruism and emotions

Emotions play an important role in the concept of psychological mechanisms. According to evolutionary psychology, humans are equipped with *mental modules*, or *psychological mechanisms*. These psychological mechanisms have evolved to cope with recurrent situations in the ancestral environment (Cosmides and Tooby 2000; Crawford 1998). Whenever an individual is confronted with a cue signaling such a situation, the mechanism is triggered and the appropriate responses become salient (Symons 1992; Tooby and Cosmides 1990b). Emotions function to link the ancestrally appropriate behavioral response to a specific adaptive problem (see also Frijda 1986; Nesse, 1990; Plutchik 1980). For example, the cue "large fanged animal" activates the emotion of fear, which prepares the organism for the appropriate response: to flee. In addition to the basic emotions of fear, joy, anger and sadness, also the secondary, or social emotions, are attributed with specific functions. For example, guilt is triggered by the subject's wrong doing of another person, and functions to urge reparation of the relationship (Fessler and Haley 2003; Parker 1998). Jealousy functions to warn people that their reproductive partner offers too much attention to a potential rival (either sexually or in terms of

[1] This chapter has been submitted for publication (c-authored with Frans N. Stokman).

resources) (Buss 2000). And according to Leary (1999), low self-esteem warns the subject that he is not accepted by his group and needs to mend this.

This paper focuses on the emotions accompanying reciprocal altruism. Although many authors have suggested the relevance of specific emotions for reciprocal altruistic behavior, empirical work is scarce. Using two mechanisms of reciprocal altruism as a starting point, the first being triggered by an imbalanced relationship and the second by the need of the other person, we will formulate hypotheses about the role of emotions in reciprocal altruistic behavior. Hypotheses will be tested by presenting subjects with dilemmas involving cues from both mechanisms, which are expected to trigger different emotional and behavioral responses.

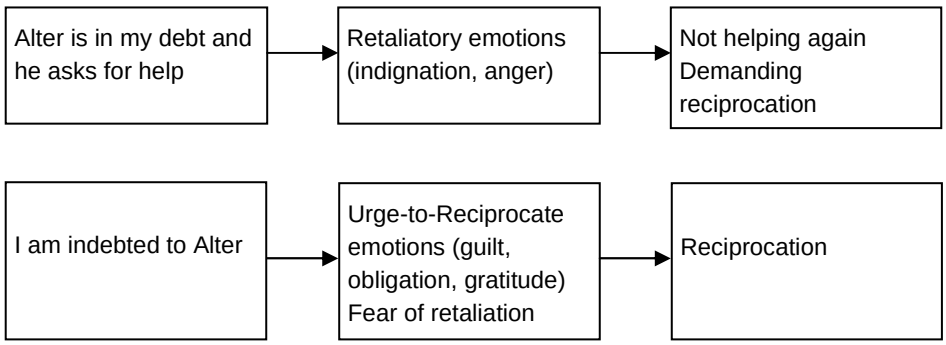
1.1 The scorekeeping mechanism

In his seminal paper, Trivers (1971, p. 35) defines *altruistic* behavior as behavior that benefits another organism's inclusive fitness while being detrimental to the organism performing the behavior. The presence of such behavior between non-related individuals, especially among humans, seems to contradict the principles of evolution. Trivers argues that such behavior is adaptive to the extent that the performer of the behavior keeps track of whether the recipient repaid him or not, and if not, curtails all future benefits to this individual. If all individuals are exposed to the same risk of needing help, in the end, reciprocal altruists are better off than non-altruists. For the human case, Trivers draws an outline of a psychological system underlying reciprocal altruism, in which an important role is played by specific emotions. Positive emotions like friendship and liking are presented as emotions motivating altruistic behavior. On the other hand, moralistic aggression and indignation are triggered by the absence of a reciprocal benefit, and function to stop one from providing the recipient with any future benefits, as well as punish, or threaten to punish, the recipient. Gratitude functions as to regulate one's response to altruistic acts, and guilt leads someone who has cheated to make up for his misdeed and to behave reciprocally in the future. Other emotions suggested by Trivers are sympathy (which motivates altruistic behavior as a function of the plight of the recipient), and trust and suspicion (which helps one to detect possible cheaters).

Although the psychological system provided by Trivers includes a considerable number of emotions expressing a willingness to help and an interest in the other person's needs, later scholars have focused on the avoidance of being cheated. Thus, in general, the psychological mechanism of reciprocal altruism is

described as a mechanism for *scorekeeping* (e.g., Cosmides and Tooby 1992; McElreath et al. 2003). This mechanism is very similar to the basic assumptions of the social psychological tradition of equity theory (Walster et al., 1978), according to which individuals try to avoid situations in which the ratio of outputs and inputs associated with a relationship is either larger of smaller than the other person's ratio.

Figure 5.1: Scorekeeping mechanisms (avoiding underbenefiting and avoiding overbenefiting)



The central cue of the scorekeeping mechanism is the difference between benefits received and benefits provided. The resulting behavior is aimed at recovering or maintaining this balance, in the case of both underbenefiting and overbenefiting. Thus, if someone else has received more than he has given back, retaliatory emotions like indignation and anger are triggered, leading to behavior aimed at recovering the balance between benefits provided and received (Nesse 1990; Parker 1998; Trivers 1971). On the other hand, the opposite situation is harmful too. To prevent others from considering me a cheater, I have to avoid that I receive more from them than I return. Therefore, overbenefiting from a person triggers urge-to-reciprocate emotions like obligation, gratitude, guilt, and fear of retaliation, resulting in behavior aimed at recovering balance (Nesse 1991, p. 277; Parker 1998, p.127; Trivers 1971). See Figure 5.1.

1.2 The bonding mechanism

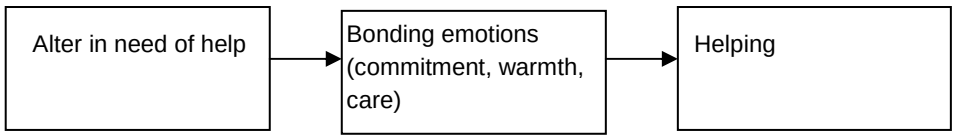
A number of scholars have criticized the one-sided emphasis on scorekeeping. For example, Kiyonary et al. (2000) argue that cooperation not only requires a cheater detection mechanism, but also a social exchange heuristic, or a *willingness to cooperate*. According to Tooby and Cosmides (1996), scorekeeping behavior is restricted to the exchange domain, which is characterized by explicit contingent exchange and turn-taking reciprocation. In contrast, the altruistic adaptations in the friendship domain do not map unto the structure of tit for tat or any other standard model of reciprocal altruism, they argue. Instead, friendships are characterized by a spontaneous pleasure to help the other, without looking for a contingent return (p. 131, 139; see also Silk 2003). Moreover, using simulation data, De Vos and coworkers (2001; this dissertation, Chapter 3) show that a strict scorekeeping strategy is vulnerable in an unpredictable environment, where actors do not get in distress neatly in turn. They distinguish between two reciprocal altruistic strategies, one guided by the rule to minimize the difference between benefits received and benefits provided (called Keeping Books Balanced); the other characterized by the tendency to return to those actors with whom one has interacted most frequently (called Commitment). Their simulations show that if the risk of getting in need of help is high, actors using a Commitment strategy are more successful in invading a population of non-cooperative actors than are actors using a Keeping Books Balanced strategy.

Similar distinctions have been made by sociologists and social psychologists. Clark and Mills (1979; Clark and Grote 2003) distinguish between exchange relationships and communal relationships. Communal relationships are characterized by mutual concern about each other's welfare and a positive attitude towards benefiting the other when a need exists. Exchange relationships, on the other hand, are characterized by the obligation to reciprocate a received benefit with a comparable return benefit. Clark and Mills hypothesize that individuals have communal relationships with family members, romantic partners and friends, whereas relationships with acquaintances, strangers and business partners pertain to the domain of exchange relationships. The results of their experiments demonstrate that towards (potential) friends or romantic partners, subjects are less likely to keep track of benefits provided and benefits received, and show more liking if the other does not keep tracks of benefits provided and benefits received, compared to strangers or persons who are not available for friendships or romantic partnerships (Clark 1984; Clark and Mills 1979). Fiske (1992) proposes four universal forms of sociality, of which communal sharing is identical to Clark and

Mills' communal relationship, whereas both equality matching, in which people keep track of the imbalances among them, and market pricing, where all relevant features and components are reduced to quantitative utilities, can be considered part of Clark and Mills' exchange relationship (the fourth form of sociality Fiske distinguishes, authority ranking, is not relevant here). Moreover, Deutsch (1975) distinguishes between different norms of distributive justice. The equity norm, according to which a person's received benefits should be proportional to the costs he has made, is similar to the operation of an exchange relationship. In contrast, the need norm, according to which a person should be rewarded according to his needs, applies to the workings of a communal relationship. In a study by O'Connell (1984), the presence of different norms governing exchange behavior was tested among people who built their own houses. The results show that benefits exchanged between kin and friends, in contrast to benefits exchanged on the market-place, are governed by non-instrumental concern and the need norm.

In sum, there are many indications for the presence of an additional mechanism of reciprocal altruism. In contrast to the scorekeeping mechanism, this mechanism is triggered by the other person's need, rather than by an unbalance in scores. The relevant emotions are those expressing an interpersonal bond, and a desire to help others in need. Because of the focus on the bond between individuals, we use the term bonding mechanism (see Figure 5.2).

Figure 5.2: Bonding mechanism



1.3 Research questions and expectations

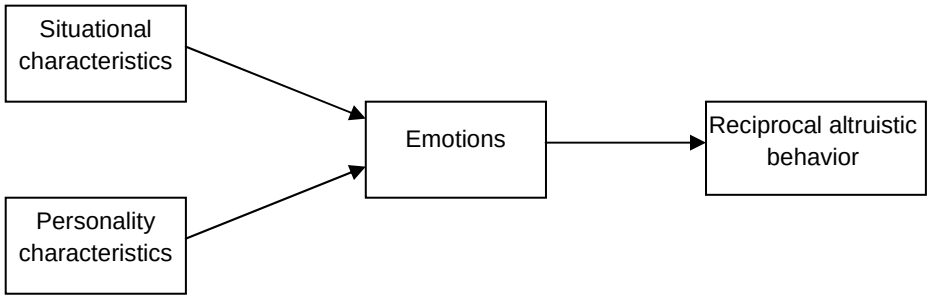
Two questions will be addressed. First, what is the relation between bonding emotions and behavioral responses, and scorekeeping emotions and behavioral responses, respectively? And second, do emotions play a mediating role between cues and behavior? These questions are addressed by presenting subjects with situations containing cues for both the bonding and the scorekeeping mechanism, thereby posing a dilemma between bonding and scorekeeping behavior. All situations involve both a needy person requesting for help, and an unbalance in

benefits received and benefits provided – either an unbalance in which the subject is underbenefiting, or one in which the subject is overbenefiting. Based on the descriptions of the two mechanisms, we expect high levels of bonding emotions towards the needy person, like commitment and warmth, to increase the tendency to help. In contrast, in the dilemma between helping a needy one and avoiding underbenefiting, high levels of retaliatory emotions, like anger and indignation, are expected to correlate with a refusal to help. On the other hand, in the dilemma between helping a needy one and avoiding overbenefiting, high levels of obligation, guilt, gratitude and fear of retaliation towards the person to whom one is indebted, are expected to correlate with reciprocating behavior. (Note that in the last situation, there is only a dilemma if the needy one is a *different* person than the person from whom one is overbenefiting).

Second, if emotions play a mediating role between cues and emotions, the effect of situational characteristics on an individual's behavioral response should be explained by the emotions experienced by this individual. Two situational characteristics will be investigated: the Object of help and the Relationship with the interaction partner. Both situational characteristics are varied between a typical exchange characteristic and a typical communal characteristic. Thus, the object of help is varied between providing assistance in the case of illness and the lending of money, and the relationship with the interaction partner is varied between a good friend and an acquaintance. If emotions play a mediating role, the effects of both the object of help and the relationship with Alter on behavioral response should be fully accounted for by the emotions triggered by these situational characteristics.

Finally, since the social psychological literature on helping behavior has given a great deal of attention to the effect of personality, also a number of personality characteristics are taken into account. Experiments have demonstrated positive effects of prosociality, responsibility, internal control, and empathy on willingness to help (Eisenberg et al. 1994; McClintock and Allison 1989), as well as on cooperative behavior in prisoner's dilemma games (Van Lange 1999) and reward allocation decisions (Perugini and Galluci 2001). In addition, individuals who have actually engaged in helping behavior (rescuing Jews; providing first aid after an accident) scored higher on internal control and social responsibility (Bierhoff et al. 1991; Oliner and Oliner 1988). However, none of these studies have investigated the role of emotions in the relation between personality characteristics and helping behavior. As in the case of situational characteristics, we expect the effect of personality characteristics on reciprocal altruistic behavior to be mediated by emotions. Figure 5.3 shows the complete model.

Figure 5.3: Theoretical model of the mediating role of emotions



2 Methods

Subjects

Subjects were 402 first-year psychology students, who had to spend three half days filling out questionnaires as part of their curriculum. The relevant questionnaire was scheduled halfway through the first day and took about fifteen minutes to complete. Completed questionnaires were obtained from 391 subjects. Data from two other questionnaires, scheduled at other times during the three half days, were also included, namely a Social Value Orientation scale (N=386), and a Justice Sensitivity scale (N=385). Mean age was 20 years (sd=4); 73% of the subjects were of the female sex.

Experimental design

Subjects were presented with three scenarios about a situation in which they were being asked for help by one or two persons they knew. All scenarios contained on the one hand cues for the bonding mechanism (someone in need for help), and on the other hand cues for the scorekeeping mechanism (an imbalance in benefits received and provided). Thus, they formed *dilemmas* between helping a needy person and avoiding an unbalanced relationship. Behavioral response was measured on a four-point scale, ranging from a definite scorekeeping response to a definite bonding response. This dilemma structure made it possible to investigate which and to what degree personality, situational and emotional variables predict a subject's decision for a bonding response as opposed to a scorekeeping response.

To control for order-effects, the order of the dilemmas was randomly varied. Immediately following the scenario, subjects had to report how they would feel towards the requester(s) in the story. Next, they were asked what they would do. Finally, subjects were asked to estimate how the requester in the story would feel if they would not help him (in the case of two requesters they were asked to estimate how the requester whom they had chosen to help would feel if they *would not* have helped him).

Two situational characteristics were manipulated, namely Object of help and Relationship with Alter. First, Object of help was varied by presenting half of the subjects with scenarios concerning the lending of money, the typical object of exchange relations. In these scenarios the request for help involved a request to borrow 100 Euros because the requester's purse had been stolen. The other half received scenarios involving a more timeless object of help, namely the providing of help in the case of illness. In these scenarios, requesters asked the subject to come over the next day to take care of them. Second, subjects' Relationship with the requester(s) was varied between a typical communal relationship type and a typical exchange relationship type, namely friend and acquaintance. This was done by presenting half of the subjects with scenarios involving only "good friends", and half of the subjects with scenarios involving only "acquaintances". The question of whether these characteristics are related to helping behavior and scorekeeping behavior is dealt with elsewhere (Smaniotto et al., submitted). Here, their primary function is to generate variation in the dependent variables.

Scenarios

Two scenarios posed a dilemma between *helping a needy one* and *avoiding underbenefiting*. Both scenarios involved one actor who is in need and requests for help. In the *Debtor in need dilemma*, the requester (D) was someone who already received help from the subject recently. Helping him again would imply an increase in the imbalance of benefits received and benefits provided, and put the subject at risk of being cheated. By refusing to help, this risk would be avoided. Thus, granting the request was the typical bonding response, whereas refusing to help was the typical scorekeeping response (see Figure 5.4A).

Figure 5.4: Scenarios, including emotion and behavior measurements

A Debtor in need dilemma

Cue	Emotions	Behavior
D is in my debt and D is in need	- Emotions towards D. - Expected emotions if I don't help D (measured after behavior)	Refuse to help vs. Help

B Refuser in need dilemma

Cue	Emotions	Behavior
R has refused to help me and R is in need	- Emotions towards R. - Expected emotions if I don't help R. (measured after behavior)	Refuse to help vs. Help

C Help vs Reciprocate dilemma

Cue	Emotions	Behavior
I am indebted to C and C is mildly in need; N is seriously in need	- Emotions towards C. - Emotions towards N. - Expected emotions by the one I choose to help if I had not chosen him (measured after behavior)	Reciprocate C vs. Help N

The *Refuser in need dilemma* was included as a more literal translation of the tit for tat strategy. It was similar to the *Debtor in need dilemma*, except that the requester (R) was someone who had recently refused to grant a request for help on the subject's part. Again, helping this person would put a subject at risk of being cheated. By refusing to help one would retaliate his previous behavior.

To emphasize the seriousness of the requesters' need for help, in both the *Debtor in need* and the *Refuser in need dilemma*, subjects were informed that the requesters did not know many people whom they could appeal to. Behavioral response was measured on a four-point scale, with answering categories "definitely not helping", "probably not helping", "probably helping", and "definitely helping" (see Figure 5.4B).

The third scenario posed a dilemma between *helping a needy one* and *avoiding overbenefiting* (*Reciprocate vs help dilemma*). In contrast to the previous dilemmas, it was

impossible to devise a dilemma between avoiding overbenefiting and helping a needy one if only one requester is involved. If a person to whom I am indebted is in need, both the bonding and the scorekeeping mechanism would respond with providing help. Therefore, a scenario involving two requesters was devised, where the dilemma consisted of which requester to provide benefits to. In this scenario both actors requested for help at the same time. The first requester (the creditor, C) recently granted a similar request for help by the subject. However, in contrast to the second requester (the needy one, N), he was only mildly in need. Thus, in the money context C asked for repayment of 100 Euros because he wanted to buy new clothes, whereas N asked to borrow 100 Euros because his purse had been stolen. Similarly, in the illness context C asked for assistance because he had caught a touch of flu, whereas N's illness was described as more serious, preventing him from leaving the house. Therefore, if the subject chose to reciprocate C, this would indicate that he attached a higher priority to avoiding overbenefiting. If he chose to help N, this would indicate a preference for helping someone who is in need. Again, a four-point scale was used, with answering categories "definitely reciprocating C", "probably reciprocating C", "probably helping N", and "definitely helping N". Subjects were informed that they did not have enough resources to provide benefits to both requesters, that they had known both requesters for about an equally long period, that C and N earned about the same income, and that they did not know much people whom they could appeal to (see Figure 5.4C).

Measurement of emotions

Emotions were measured using self-reports. Although reliability of self-reports of emotions has been questioned – critics have put forward problems of memory, self-deception, social desirability and individual differences in lexical meanings (Lazarus 1991, p. 450; Plutchik 2003, p. 17), they are generally considered a valuable option (Lazarus 1991; Ortony et al. 1988, p. 9; Wallbot and Scherer 1989), especially since the possibilities of taking objective measurements of emotions are still in their infancy. As yet, no clear-cut relations between complex emotion states and physiological responses have been established (Plutchik 2003, p. 141-143).

For every requester, subjects were instructed to fill out a list of emotions. All emotion lists contained the same fourteen emotions that were selected to represent Bonding emotions (Commitment, Warmth, Worriedness), Retaliatory emotions (Contempt, Anger, Disappointment, Indignation, Irritation), and Urge-to-Reciprocate emotions (Gratitude, Obligation, Guilt). Three additional emotions

functioned as filler-items (Sadness, Uncomfortableness, Understanding). Subjects were instructed to indicate the degree to which they would experience the concerning emotion on a four-point scale (answering categories "not at all", "a little", "quite", "strong"). Furthermore, after the behavioral response measure they were presented with a final emotion list containing the same emotions on which they had to rate the emotions they would expect the target person to experience if they had not helped (in case of the Recriprocate vs help dilemma, the target person was the one they had chosen to help). Of these lists the Expected Retaliatory emotions were used as a measure of fear of retaliation.

Principal Factor analyses were conducted to confirm the hypothesized categories (see Appendix 3). Emotion responses to the *Debtor in need* and the *Refuser in need dilemmas* were combined (see Section 3.1). The Retaliatory emotions and the Expected Retaliatory emotions formed clear factors in all emotion lists. Reliability analyses yielded alphas ranging from 0.78 to 0.90. Warmth, Commitment and Worriedness were part of the same factor in most of the emotion lists, but Worriedness showed consistently lower factor loadings. In contrast to expectations, Gratitude was also placed in this factor. As in the case of Worriedness, factor loadings were generally low. Moreover, communality-values of Gratitude were occasionally extremely low, indicating that the variance in Gratitude responses was not well explained by the common factors. Therefore, a two-variable Bonding variable was constructed, consisting of Warmth and Commitment. Alphas ranged between 0.67 and 0.75. There appeared to be no cluster of Urge-to-Reciprocate emotions. Obligation, Gratitude and Guilt never appeared as a single cluster. They were sometimes categorized in the Bonding emotions factor and sometimes in different factors. Like Worriedness, they are treated as separate emotions in the further analyses.

Personality traits

Personality scales were administered at other times during the three half days subjects spent filling out questionnaires. The personality measures include a scale that is often associated with prosocial or altruistic behavior, namely an adjusted version of the Social Value Orientation Scale, as well as a questionnaire consisting of two scales that explicitly focus on the avoidance of underbenefiting and overbenefiting.

Prosociality. Subjects were presented with five questions from the Social Value Orientation Scale developed by Van Lange et al. (1997), which originally consisted of nine items. All five questions concerned a choice for one out of three

different distributions of a fixed amount of money, to be divided between the subject and another actor. Options always included a prosocial distribution, with both Ego and Alter getting the same amount; an individualistic option, which was, compared to the prosocial option, more beneficial to Ego and less beneficial to Alter; and a competitive option, in which, compared to the individualistic option, Ego's reward was smaller but the difference between Ego's reward and Alter's reward was larger. Instead of categorizing subjects as either prosocial, individualistic or competitive, an interval variable was created by adding up the number of prosocial answers. Since the number of competitive answers was extremely low (only five out of 386 subjects chose for the competitive option one or more times), it made no sense to use competitiveness as a separate variable.

Justice Sensitivity Victim (JS Victim). We used a six-item scale to measure subjects' sensitivity of being a victim of injustice, as developed by Schmitt et al. (1997; see also Fetchenhauer and Huang 2004). Examples of items are "I am irritated when others get the praise that should be given to me" and "I don't forget when I need to repair another person's omissions." Subjects were asked to indicate the degree to which each item applied to them on a seven-point scale. (Reliability: alpha=0.76.)

Justice Sensitivity Perpetrator (JS Perpetrator). Subjects' sensitivity of being a perpetrator of injustice was measured by the mirrored version of the JS Victim Scale, also developed by Schmitt et al. (1997). Items include "My conscience objects when I get the praise that should be given to someone else" and "I don't forget when someone else has to repair my omissions". (Reliability: alpha=0.75.)

3 Results

Although the dependent variable was measured on a quasi interval scale, linear regression analyses would yield unreliable results due to highly skewed distributions of both emotion and behavior responses (see Appendix 4). Instead, behavioral response variables were dichotomized and used as dependent variables in a series of logistic regression analyses. In the *Debtor in need* and *Refuser in need dilemmas* answering categories were recoded into *helping* versus *not helping*, and in the *Reciprocate vs help dilemma* answering categories were recoded into *helping N* versus *reciprocating C*. Rather than using subjects' scores on the independent variables to predict the scores on behavioral response, logistic regression analysis predicts the *probability of helping* (as opposed to not helping/ reciprocating). Separate analyses

were performed for the scenarios posing a dilemma between helping a needy one and avoiding underbenefiting (*Debtor in need* and *Refuser in need dilemmas*) and for the scenario posing a dilemma between helping a needy one and avoiding overbenefiting (*Reciprocate vs help dilemma*).

3.1 Avoiding underbenefiting versus helping

The two scenarios posing a dilemma between helping a needy one and avoiding underbenefiting were analyzed together. To avoid being forced to use a repeated measures statistical design, from each subject only the responses on the dilemma emerging first in the questionnaire was included in the analyses. Next, a dummy variable was created to indicate whether the requester was a debtor or a refuser. Guilt and Gratitude were excluded from the analyses because of the small number of subjects reporting Guilt or Gratitude in either the *Debtor in need* or the *Refuser in need dilemma* (more than 90% of subjects were in the two lower categories; see Appendix 4).

Table 5.1 shows the results. To facilitate interpretation, odds values [Exp(b)] rather than logodds values are shown. Odds values denote the *probability of helping as a fraction of the probability of not helping*. For example, an odds of 1 indicates that the probability of helping equals the probability of not helping, that is, no effect of the concerning predictor whatsoever. A value larger than 1 means that with each additional unit of the predictor, the odds of helping versus not helping increases. A value smaller than 1 indicates that with each additional unit of the predictor, the odds of helping versus not helping decreases. To facilitate comparison of negative and positive effects, values smaller than 1 are denoted as $[1/Exp(b)]^{-1}$. For example, in the case of Bonding emotions (Model 1), each additional unit of emotion leads to a multiplication of the odds of helping by 2.34. The effect of Retaliatory emotions is larger in size and opposite in direction: with each additional unit the odds of helping is multiplicated by 4.02^{-1} , or 0.25.

Table 5.1: Results of logistic regression analyses on the Debtor in need and Refuser in need dilemmas. Values denote the odds of helping versus not helping [Exp(b)].

	Model 1	Model 2	Model 3	Model 4
Constant	1.00	4.27	1.20	500.00^{-1}**
Dilemma (debtor)		2.11	1.18^{-1}	1.94^{-1}
Object (illness)		2.27*	2.41*	2.13
Relationship (friend)		1.51	1.31	1.43
Sex (female)		1.02^{-1}	1.84^{-1}	8.45
JS Victim		1.08^{-1}**	1.04^{-1}	1.05^{-1}
JS Perpetrator		1.02	1.03	1.04
Prosociality		1.18	1.12	3.19**
Dilemma by Prosociality		1.31^{-1}*	1.34^{-1}	1.16^{-1}
Dilemma by Object		32.67**	10.63*	11.90*
Bonding emotions	2.34**		1.88*	2.21*
Retaliatory emotions	4.02^{-1}**		4.61^{-1}**	1.77^{-1}
Worriedness	1.09		1.29	8.21**
Obligation	2.25**		2.45**	2.26**
Exp Retaliatory emotions	1.44		1.64	1.76
Sex * Retaliatory emotions				3.61^{-1}*
Prosociality * Worriedness				1.67^{-1}**
N	379	370	361	361
-2 Log likelihood	319.11	336.60	261.11	243.37
Hosmer Lemeshow Test (Chi^2)	2.15; df=8 (ns)	12.52; df=8 (ns)	10.36; df=8 (ns)	8.91; df=8 (ns)

Note: Emotions were measured on a 4-point scale with 1=not at all and 4=strong.
** Wald statistic significant at $p<0.01$; * Wald statistic significant at $p<0.05$

Scorekeeping and bonding emotions in a dilemma between helping and avoiding underbenefiting

To answer the first research question, regarding the effects of Bonding emotions and Scorekeeping emotions on behavioral responses, a model was estimated with the emotions as independent variables and behavioral response as dependent variable (Table 5.1, Model 1). We expected that Bonding emotions and Worriedness trigger helping behavior, whereas Retaliatory emotions lead to

behavior aimed at avoiding an unbalance (i.e., refusing to help). In other words, a high degree of Bonding emotions and Worriedness should increase the odds of helping, and a high degree of Retaliatory emotions should decrease the odds of helping.

The results show that, in accordance with expectations, Bonding emotions have a positive effect on the odds of helping and Retaliatory emotions have a negative effect. The effect of Worriedness is slightly positive but not significant. Obligation, which was expected to be only effective in the dilemma between helping a needy one and avoiding overbenefiting, increases the odds of helping. Also Expected Retaliatory emotions increase the odds of helping, although the effect is not significant. This suggests that the designated Urge-to-Reciprocate emotions are not exclusively related to avoiding overbenefiting. A possible interpretation is that individuals feel that they have a strong moral obligation to help a person in need, which is both expressed by the emotion of obligation and, to a lesser degree, by the expectation that the other person will be resentful if they do not help.

The role of emotions in a dilemma between helping and avoiding underbenefiting

Models 2 to 4 center on the question whether emotions play a mediating role between personality and situational variables on the one hand, and behavioral responses on the other hand. To answer this question we need to compare logistic regression models when excluding and including the emotion variables. If emotions play a purely mediating role, the following conditions should be fulfilled (e.g., Baron and Kenny 1986):

1) The model including the emotion variables has a better fit than the model excluding the emotion variables.
2) The logistic regression coefficients of the situational and personality variables decrease when including the emotion variables.
3) The logistic regression coefficients of the emotion variables do not decrease when controlling for the personality and situational variables.
4) There are no interaction effects of emotion variables and personality or situational variables. If that were the case, this would point to a moderating rather than a mediating role of emotions.
5) When conducting additional regression analyses with the significant emotions as dependent variables, the personality and situational variables that were significant in the logistic regression analyses show significant effects.

Model 2 contains the effects of the situational and personality variables. The Dilemma variable, Object of help, Relationship with Alter and Sex were inserted as dummy variables, whereas JS Victim, JS Perpetrator and Prosociality were treated as interval variables. In addition, all possible 2-way interaction terms were subjected to a stepwise selection procedure. As shown in Model 2, there are significant main effects of Object of help and JS Victim. The odds of helping is 2.27 times as large in the illness context as it is in the money context. The negative effect of JS Victim indicates that subjects who are more sensitive to being a victim of injustice are less likely to help. As appears from the absence of further significant effects, the odds of helping does not differ for friends versus acquaintances and females versus males, nor does it change with increasing scores on JS Perpetrator or Prosociality. In addition, there are two significant interaction effects, one concerning Dilemma and Prosociality and the other of Dilemma and Object of help.

Figures 5.5 and 5.6 depict the probability of helping as a function of Prosociality and Object of help, respectively. Odds values were converted into probabilities using the formula:

$$\text{Probability of helping} = \frac{Exp(a + b_1 * x_1 + b_2 * x_2 + \ldots + b_n * x_n)}{Exp(a + b_1 * x_1 + b_2 * x_2 + \ldots + b_n * x_n) + 1}$$

The concerning *x*'s were substituted with different values of Prosociality and Dilemma (Figure 5.5) and Object of help and Dilemma (Figure 6). To control for the remaining variables, all other x's were substituted with their mean values. As is shown in Figure 5.5, the negative interaction effect of Dilemma and Prosociality indicates that Prosociality only affects responses in the *Refuser in need dilemma*. In the *Debtor in need dilemma*, the probability of helping is very high, regardless of the degree of Prosociality. Moreover, the positive interaction effect of Dilemma and Object of help indicates that whereas subjects are equally likely to grant a request for *money* by a Debtor or a Refuser, they are less likely to grant a request for *assistance in the case of illness* if it concerns a Refuser than if it concerns a Debtor (see Figure 5.6). This suggests that being ill is considered such an urgent need that a previous refusal is less acceptable, and more likely to evoke punishment in the form of withholding help, compared to indebtedness.

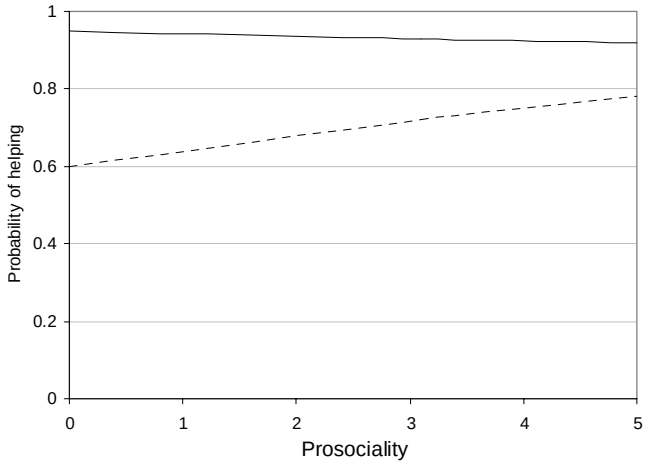


Figure 5.5: Probability of helping as a function of Prosociality.

Key: Debtor in need Refuser in need

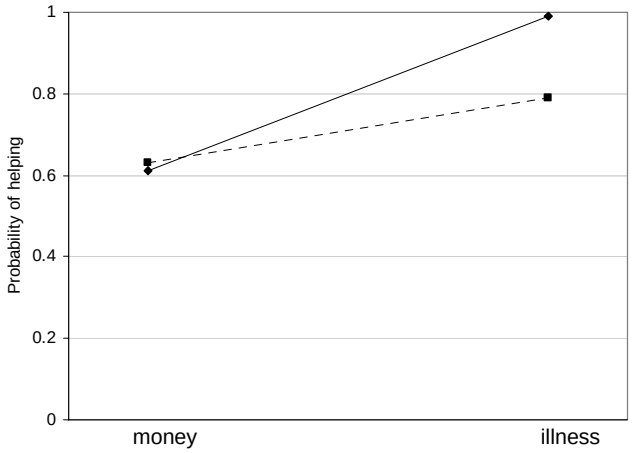


Figure 5.6: Probability of helping as a function of Object of help.

Key: Debtor in need Refuser in need

Model 3 includes situational and personality variables as well as the emotion variables from Model 1. The first three requirements for the mediating role of emotions prove to be fulfilled. First, the sharp decline of the -2 log likelihood ratio indicates a strong increase in model fit (Chi^2=75.49; df=5; p<0.001). Second, there is a general decrease in the effects of the situational and personality variables. The main effect of JS Victim and the interaction effect of Dilemma and Prosociality lose significance. The main effect of Object of help remains at the same level, but its interaction effect with Dilemma decreases substantially. And third, all emotions that were significant in Model 1 maintain significance.

The fourth requirement for the mediating role of emotions is tested in Model 4. If emotions have a mediating role between situational and personality characteristics, they should have identical effects within each category of the situational and personality variables. In other words, there should be no significant interaction effects. The presence of significant interaction effects would imply that the emotions *operate differently* within the different categories of the personality and situational characteristics, rather than *explain* the effect of the personality and situational characteristics. Model 4 contains all variables of Model 3, as well as those two-way interaction terms of emotions and situational or personality variables that proved to be significant in a stepwise selection procedure. In contrast to expectations, there are two significant interaction effects: a negative interaction effect of Sex and Retaliatory emotions and a negative interaction effect of Prosociality and Worriedness. Both of these will be interpreted in the next section.

The fifth requirement for the mediating role of emotions is that the indirect effects of situational and personality characteristics are confirmed by linear regression analyses with the emotions as dependent variables. Table 5.2 shows the results of three regression analyses, with the emotions that were significant in Model 1 as dependent variables, and the situational and personality characteristics, including the two interaction effects, as independent variables.

The results confirm the presence of some of the suggested indirect effects. Thus, the indirect effect of JS Victim on the odds of helping appears to be due to a negative effect on Bonding emotions (b=-0.02; p<0.01) and a positive effect on Retaliatory emotions (b=0.03; p<0.01). The effect of the interaction term Dilemma by Object is spread over all three emotion variables: compared to *Refusers in need of money*, *Debtors in need of nursing* elicit more Bonding emotions (b=0.53; p<0.01), less Retaliatory emotions (b= -0.47; p<0.01) and more Obligation (b=0.62: p<0.01). Unexpectedly, the interaction effect of Dilemma and Prosociality on behavioral response is not reflected in these additional regression analyses: although prosocial

subjects report significantly less Retaliatory emotions as compared to less prosocial subjects, none of the emotion variables is affected by the interaction of Dilemma and Prosociality.

Table 5.2: Results of three linear regression analyses with emotions as dependent variables and situational and personality characteristics as independent variables. Underbenefiting dilemmas. Values denote B-coefficients

	Bonding emotions	Retaliatory emotions	Obligation
Constant	2.06**	1.76**	1.04**
Dilemma (Debtor)	0.12	-0.54**	0.36*
Object (illness)	0.12	-0.05	0.07
Relationship (friend)	0.18**	-0.04	0.09
Sex (female)	-0.09	-0.09	0.17
JS Victim	-0.02**	0.03**	0.00
JS Perpetrator	0.00	-0.01	0.01
Prosociality	-0.00	-0.05*	0.03
Dilemma by Prosociality	0.02	0.05	-0.05
Dilemma by Object	0.53**	-0.47**	0.62**
R^2	0.25	0.37	0.19
N	368	367	371

Note: Emotions were measured on a 4-point scale with 1=not at all and 4=strong.
* = significant at $p<0.05$; ** = significant at $p<0.01$

Interaction effects of emotions in a dilemma between helping and avoiding underbenefiting

In contrast to expectations, there were two significant interaction effects of and emotion and an independent variable. The negative interaction effect of Sex and Retaliatory emotions indicates that the presence of Retaliatory emotions decreases the odds of helping to a higher degree among women than among men (see Figure 5.7), suggesting that women act more on their Retaliatory emotions than men do.

The negative interaction effect of Prosociality and Worriedness should be interpreted against the background of positive main effects of both Prosociality and Worriedness. Figure 5.8 shows the probability of helping as a function of Worriedness. By substituting the minimum, average and maximum value on Prosociality in the logistic regression formula, different curves were acquired for

subjects low, average and high on Prosociality. As shown in Figure 5.8, the positive effect of Worriedness is restricted to subjects low on prosociality. Among subjects scoring average or high on prosociality the degree of Worriedness does not make a difference; they tend to help the needy one anyway.

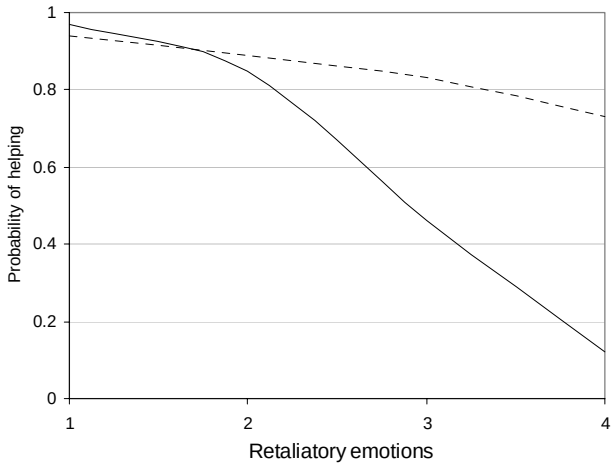


Figure 5.7: Probability of helping as a function of Retaliatory emotions.
Key: - - - - male —— female

Conclusion

In sum, the results of the dilemma between helping and avoiding underbenefiting provide support to the hypothesis that Bonding emotions increase helping behavior. Worriedness also increases helping behavior, but only among subjects scoring low on prosociality. Also in line with the hypotheses is the negative effect of Retaliatory emotions, although this effect is larger for women than for men. The unexpected effect of Obligation suggests that this emotion is not an exclusive Urge-to-Reciprocate emotion. The mediating role of emotions is supported, although the representation of a strict model in which the effects of situational and personality characteristics on behavioral response are completely accounted for by emotions is not confirmed. After including the emotion variables, model fit increases drastically and the effects of personality and situational characteristics generally decrease, but they do not disappear completely. Furthermore, the presence of two interaction effects of emotions and personality characteristics

suggest that the mediating role of emotions mainly concerns situational characteristics.

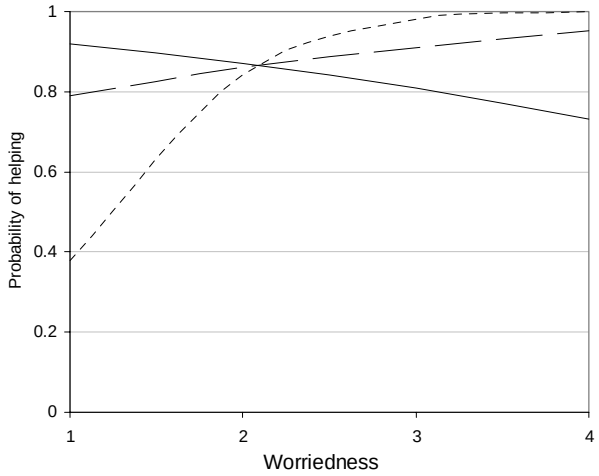


Figure 5.8: Probability of helping as a function of Worriedness.
Key: Prosociality low average high

3.2 Avoiding overbenefiting versus helping

The same procedure of model construction was followed for the dilemma between helping a needy one and avoiding overbenefiting. Since there was only one scenario presenting this dilemma, all responses were included in the analyses. Furthermore, as the concerning scenario involved two requesters, and posed a dilemma between *whom* to help, the number of emotion variables was doubled and the presented odds values denote *the probability of helping the needy one (N) as a fraction of the probability of reciprocating the creditor (C)*. Retaliatory emotions towards C and N, as well as Gratitude towards N were not included in the logistic regression analyses because of the small amounts of subjects reporting these emotions (more than 90% of subjects are in the two lower categories; see Appendix 4). Expected Retaliatory emotions were also excluded since the target person of these emotions varied according to which requester the subject had chosen to help. However, a comparison of the mean value on Expected Retaliatory emotions by those subjects who decided to help N with those subjects who decided to reciprocate C showed no difference (both mean values were 2.25).

Table 5.3: Results of logistic regression analyses on the Reciprocate vs help dilemma. Values denote the odds of helping N versus reciprocating C [Exp(b)].

	Model 1	Model 2	Model 3	Model 4
Constant	1.61^{-1}	1.65	1.49	125.00^{-1}
Object (illness)		9.28**	7.23**	2.78^{-1}
Relationship (friend)		1.02^{-1}	1.29^{-1}	1.10
Sex (female)		1.08	1.33	1.75
JS Victim		1.04^{-1}	1.06^{-1}*	1.11
JS Perpetrator		1.00	1.00	1.00
Prosociality		1.03	1.04	2.00*
Bonding emotions towards N	2.57**		3.41**	4.55**
Bonding emotions towards C	1.34^{-1}		1.73^{-1}	2.22^{-1}*
Worriedness towards N	1.47		1.28	2.52*
Worriedness towards C	1.72*		1.13^{-1}	1.35^{-1}
Obligation towards N	3.82**		3.18**	3.43**
Obligation towards C	4.59^{-1}**		3.83^{-1}**	4.27^{-1}**
Guilt towards N	2.69^{-1}**		2.48^{-1}**	5.71^{-1}**
Guilt towards C	1.44		1.79**	15.47**
Gratitude towards C	1.07		1.06	1.11
Object * Obligation towards C				3.09*
Relationship * Obligation towards C				2.50^{-1}*
Relationship * Guilt towards N				4.56**
JS Victim * Guilt towards C				1.08^{-1}*
Prosociality * Worriedness towards N				1.24^{-1}*
N	366	355	349	349
-2 Log Likelihood	318.95	381.74	277.64	249.55
Hosmer Lemeshow Test (Chi^2)	13.309; df=8 (ns)	5.99; df=8 (ns)	8.53; df=8 (ns)	8.53; df=8 (ns)

Note: Emotions were measured on a 4-point scale with 1=not at all and 4=strong.
** Wald statistic significant at $p<0.01$; * Wald statistic significant at $p<0.05$

Scorekeeping and bonding emotions in a dilemma between helping and avoiding overbenefiting

We expected the odds of helping N to be positively affected by Bonding emotions and Worriedness towards N and not to be affected by Bonding emotions and Worriedness towards C. As shown in Table 5.3 (Model 1), Bonding emotions towards N increase the odds of helping N, whereas Bonding emotions towards C lead to a non-significant decrease in the odds of helping N. In contrast to expectations, both Worriedness towards N and C raise the odds of helping N, but only the second is significant. Urge-to-Reciprocate emotions towards C were expected to lower the odds of helping N, whereas Urge-to-Reciprocate emotions towards N should have no significant effects. Model 1 shows that, as expected, Obligation towards C lowers the odds of helping N. However, as in the dilemma between helping a needy one and avoiding underbenefiting, there is also a positive effect of Obligation towards the needy one. Guilt shows the opposite picture: Guilt towards C is associated with a non-significant increase in the odds of helping N, whereas Guilt towards N is associated with a decrease. A possible explanation is that subjects did not report Guilt as a consequence of the cues presented in the dilemma, but as an expression of awkwardness in anticipation of going to refuse the target person.[2] Finally, neither do the results provide support to the urge-to-reciprocate function of Gratitude: the effect of Gratitude towards C is positive, although it is not significant.

The role of emotions in a dilemma between helping and avoiding overbenefiting

Model 2 contains the situational and personality characteristics. A stepwise addition of all possible 2-way interaction terms did not yield any increase in fit. The only significant effect comes from Object of help. Compared to the money context, the illness context multiplicates the odds of helping N with 9.28.

The next model includes the emotion variables (Model 3). As appears from the decrease of the -2 Log likelihood ratio, the fit of Model 3 is significantly better than that of Model 2 ($Chi^2=104.10$; $df=9$; $p<0.001$), fulfilling the first requirement of the mediating role of emotions. However, compared to the analyses of the dilemma between helping and avoiding underbenefiting, there is much less support for emotions as mediators between personality and situational

[2] Pearson's correlations with the filler emotion Uncomfortableness support this interpretation. Of all emotions towards C and N, Guilt towards C correlates most strongly with Uncomfortableness towards C ($r=0.55$; $p<0.01$; two-tailed) and Guilt towards N correlates most strongly with Uncomfortableness towards N ($r=0.54$; $p<0.01$; two-tailed).

characteristics on the one hand, and behavioral responses on the other hand. First, the coefficients of the situational and personality characteristics do not decline after including the emotion variables. The effect of Object of help, which was the only significant effect in Model 2, remains at the same level. Moreover, the effect of JS Victim increases, thereby reaching significance. Second, although four emotion variables that were significant in Model 1 maintain their effects, two emotion variables change considerably in their effects when controlling for the personality and situational variables. The effect of Guilt towards C increases and reaches significance. Moreover, the puzzling effect of Worriedness towards C reverts in direction and loses significance.

Model 4 shows that the fourth requirement for the mediating role of emotions is also not fulfilled. There is a considerable number of interaction effects, mainly concerning situational characteristics.

With both the second, third and fourth requirement unfulfilled, conducting additional regression analyses is meaningless. Since there is no support for a mediating role of emotions, it makes no sense to investigate the "direct" effects of situational and personality characteristics on the emotion variables.

Interaction effects of emotions in a dilemma between helping and avoiding overbenefiting

The results of the *Reciprocate vs help dilemma* showed five significant interaction effects of emotions and situational or personality variables. The effect of Obligation towards C appears to be dependent on both Object of help and Relationship with Alter. Figures 5.9 and 5.10 depict both interaction effects when controlling for all other variables. The negative effect of Obligation towards C on the probability of helping N appears to be much stronger in the money context, as compared to the illness context (see Figure 5.9), and mildly stronger towards friends, as compared to acquaintances (see Figure 5.10). The first interaction effect is in line with the ambiguous role of Obligation. Apparently its Urge-to-Reciprocate function is restricted to the money context. The second effect suggests that if people experience Obligation towards a creditor, they are more likely to act upon it if they deal with friends than if they deal with acquaintances.

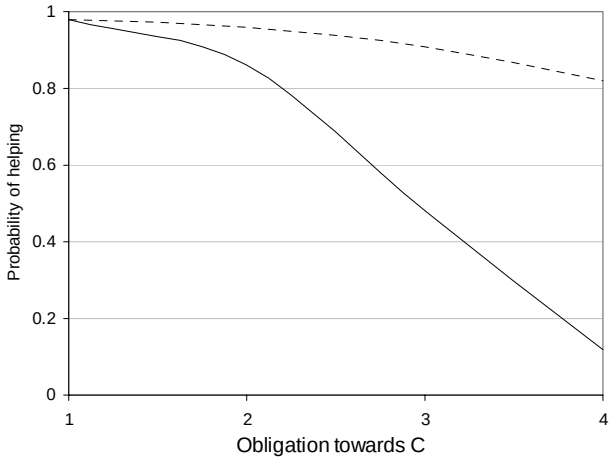


Figure 5.9: Probability of helping N (as opposed to reciprocating C) as a function of Obligation towards C.

Key: —— money - - - - illness

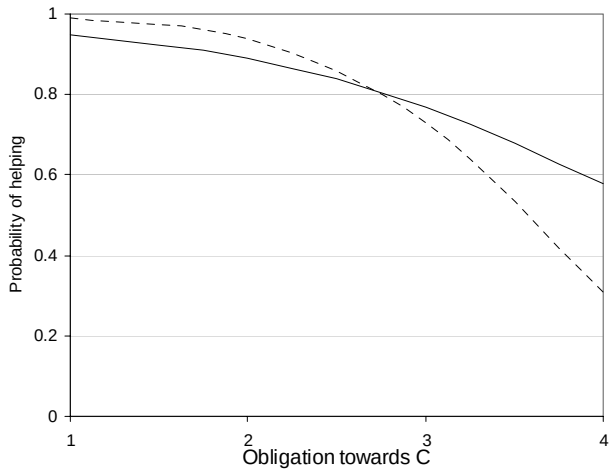


Figure 5.10: Probability of helping N (as opposed to reciprocating C) as a function of Obligation towards C.

Key: - - - - friend —— acquaintance

Furthermore, there are two interaction effects concerning Guilt. The positive interaction effect of Guilt towards N and Relationship with Alter cancels out the negative main effect of Guilt. As Figure 5.11 shows, the negative effect of Guilt towards N is confined to interactions with acquaintances, whereas there is no or hardly any effect on interactions with friends. In line with the previous interpretation of Guilt as an expression of awkwardness in the anticipation of going to refuse the target person, a plausible explanation is that if subjects decide to reciprocate C (and consequently, refuse to help N), they are more concerned if they deal with an acquaintance than if they deal with a friend, and thus, report more Guilt towards acquainted N's than towards befriended N's. Next, when plotting the negative interaction effect of Guilt towards C and JS Victim (Figure 5.12) it turns out that for subjects scoring high on JS Victim, the positive main effect of Guilt towards C on helping N turns into a negative one. It seems therefore, that among subjects who are highly sensitive to being a victim of injustice, Guilt towards C does operate in the expected way; that is, as an Urge-to-Reciprocate emotion.

Finally, the negative interaction effect of Prosociality and Worriedness towards N is similar to that in the dilemma between helping and avoiding underbenefiting: only among subjects low on prosociality is there a positive effect of Worriedness towards N. Subjects scoring average or high on prosociality are likely to help N, regardless whether they worry or not (see Figure 5.13).

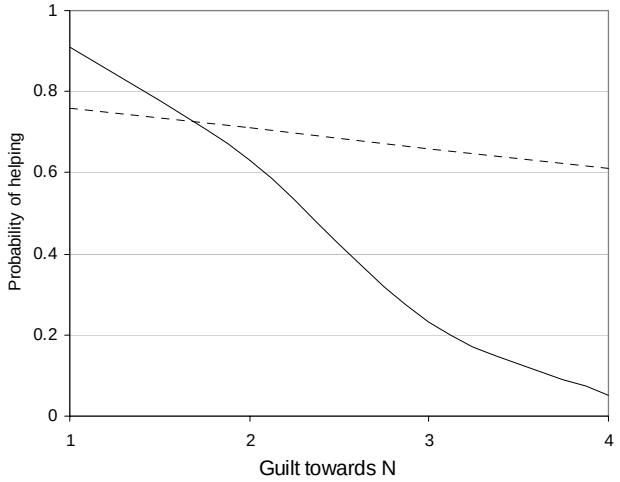


Figure 5.11: Probability of helping N (as opposed to reciprocating C) as a function of Guilt towards N.
Key: - - - - friend ——— acquaintance

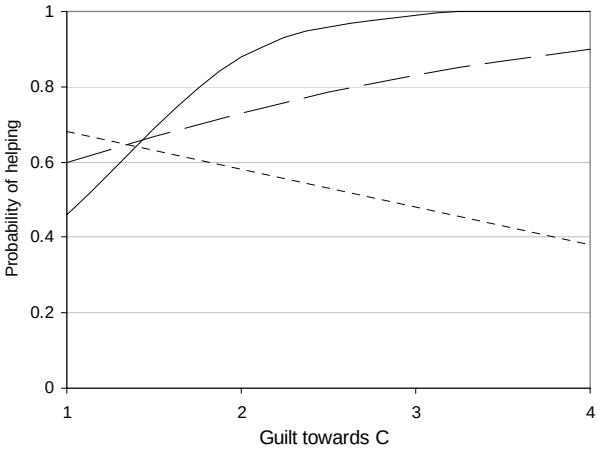


Figure 5.12: Probability of helping N (as opposed to reciprocating C) as a function of Guilt towards C.
Key: JS Victim —— low —— average - - - - high

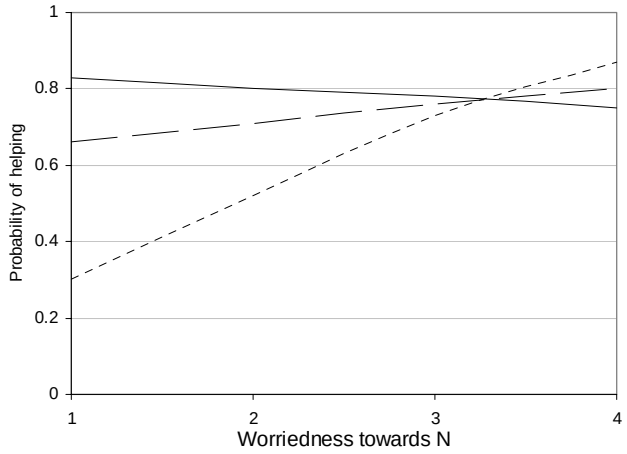


Figure 5.13: Probability of helping N (as opposed to reciprocating C) as a function of Worriedness towards N.
Key: Prosociality - - - - low —— average —— high

Conclusion

In sum, the results of the dilemma between helping and avoiding overbenefiting provide only partial support to the distinction between bonding and scorekeeping mechanisms. In line with expectations, the odds of helping N is increased by Bonding emotions towards N and not affected by Bonding emotions towards C. Furthermore, like in the dilemma between helping a needy one and avoiding underbenefiting, the positive effect of Worriedness towards N is restricted to subjects who are not very prosocial. Behavior is also influenced by Worriedness towards C, although this effect disappears when controlling for personality and situational characteristics. In addition, there is little support that Obligation, Guilt, Gratitude and Expected Retaliatory emotions lead to reciprocating. Dependent on the Object of help, Obligation is interpreted as a feeling of indebtedness towards a creditor, leading to reciprocating, or as a moral duty to help a needy one. Furthermore, only among subjects who are highly sensitive to being a victim of injustice does Guilt function as an Urge-to-Reciprocate emotion. Among those lower on JS Victim it expresses some kind of awkwardness in the anticipation of going to refuse the target person. The remaining Urge-to-Reciprocate emotions do not affect behavior.

Next, the mediating role of emotions does not receive much support. Although the inclusion of the emotions leads to a strong increase in fit, it does not lead to a decrease in the effects of situational and personality variables. There is more support for a moderating role of emotions concerning both personality and situational characteristics.

4 Overall conclusion

This study attempted to determine the role of emotions in reciprocal altruistic behavior by using dilemmas between helping a needy person and avoiding an unbalanced relationship. Hypotheses were tested regarding the relation between specific emotions and behavioral responses. Bonding emotions like Commitment and Warmth, as well as Worriedness were expected to increase the tendency to help a person in need rather than refusing him or using one's resources to reciprocate a creditor. Retaliatory emotions, including Contempt, Anger, Disappointment, Indignation and Irritation, were expected to trigger behavior aimed at avoiding underbenefiting, that is, a refusal to help. Finally, Urge-to-Reciprocate emotions, like Obligation, Guilt and Gratitude, as well as Expected Retaliatory emotions, were expected to trigger behavior aimed at avoiding

overbenefiting, that is reciprocating a creditor. Furthermore, based on the evolutionary psychological view of emotions, we predicted that emotions mediate the relation between personality and situational characteristics on the one hand, and behavioral responses on the other hand.

In general, the results of the dilemma between helping a needy one and avoiding underbenefiting were supportive to the hypotheses. A high degree of Bonding emotions increased the tendency to help a needy person, and a high degree of Retaliatory emotions decreased the tendency to help. Furthermore, all necessary conditions for the emotions to have a mediating role were fulfilled. The results of the dilemma between helping a needy one and avoiding overbenefiting were less supportive. The effects of Urge-to-Reciprocate emotions on reciprocating behavior were absent or conditional on situational or personality variables. Thus, Obligation increased the tendency to reciprocate a creditor only if the Object of help was money, and Guilt was positively correlated with reciprocating only among subjects who were highly sensitive to being a victim of injustice. In contrast, subjects who reported high levels of Gratitude or Expected Retaliatory emotions towards the creditor were not more likely to reciprocate him than subjects who were not grateful or expecting retaliation at all. Furthermore, there was no support for the mediating role of emotions.

To conclude from these results that people do not have a psychological mechanism for avoiding overbenefiting seems too rash. Since the *Reciprocate vs help dilemma* involves a situation with two requesters, and the behavioral response consists of whether to help N or to reciprocate C, rather than whether to help or not to help, it is more prone to errors, resulting in weaker relations between variables. Another possible reason for the weak results is that the Urge-to-Reciprocate emotions are less basic than the Bonding and Retaliatory emotions. Whereas the Bonding and Retaliatory emotions appear on the most basic list of primary emotions (i.e., including anger, fear, joy/love, sadness) (Plutchik 2003, p. 73), the Urge-to-Reciprocate emotions are examples of secondary or social emotions (e.g., Nesse 1990; Parker 1998). By definition, secondary emotions are less universal than basic emotions and thus will be more liable to differences in interpretation.

Limitations of the study

A possible criticism is that the emotion responses reflect only stereotypes about which emotions belong to which behavioral response (e.g., see Wallbott and Scherer 1989, p. 64). Although the questions concerning behavioral response were

presented *after* the emotions lists, it is possible that the scenarios, being about actors requesting for help, made subjects automatically reflect on their reaction to the requests, and adjust their emotion responses accordingly. This problem is inextricably linked to the use of self-reports and can only be solved if the possibilities for taking objective measurements of complex emotions increase.

Another possible criticism concerns the use of a scenario rather than an experimental design. A drawback of scenarios is that they measure what subjects say they will do rather than behavior itself. Furthermore, the cues presented in a scenario are less strong than cues administered in a laboratory situation. At first sight, both of these drawbacks seem to be absent in an experimental design. However, in the case of the present research question it is doubtful whether an experimental design would yield more valid results. First, in contrast to many experimental designs focusing on how subjects distribute or allocate resources (e.g., Ultimatum Games and Public Good Games), the present research question requires that subjects are *not anonymous*. Maintaining anonymity serves to eliminate effects of future interactions on one's present behavior towards an interaction partner, for example, the prospect of being punished for selfish behavior (Fehr and Gächter 2000). In the present research, the expectation of one's interaction partner's Retaliatory emotions is one of the variables under study. Furthermore, it makes no sense to study the effect of Relationship with Alter among anonymous subjects. On the other hand, an experimental design in which *non-anonymous* subjects have to distribute resource, such as an Ultimatum Game design, would yield responses that are strongly biased by social desirability.

Second, bringing subjects into the laboratory in pairs of *real* friends or acquaintances, and *experimentally* creating an unbalance in their relationship means a strong asymmetry in cues for Bonding emotions on the one hand and Retaliatory or Urge-to-Reciprocate emotions on the other hand. How this asymmetry will affect responses is uncertain. By using instead subjects who do not know each other and then manipulate attraction, cues for Bonding and Retaliatory or Urge-to-Reciprocate emotions would both be experimentally induced. Obviously this would evoke much lower degrees of Bonding emotions compared to a situation in which subjects have known each other for years.

In conclusion, both scenarios and experiments have their merits and drawbacks. Our understanding of the relation between Bonding, Retaliatory and Urge-to-Reciprocate emotions on the one hand and reciprocal altruistic behavior on the other hand would benefit most if both scenario and experimental designs were used.

CHAPTER 6

Conclusion

1 Introduction

This dissertation centered on two proximate mechanisms of reciprocal altruism. The scorekeeping mechanism was described as primarily directed at maintaining a balanced relationship, that is: avoiding both underbenefiting and overbenefiting with regard to one's interaction partner. The bonding mechanism, in contrast, was described as primarily focused on helping one's friends if they are in need. Evolutionary psychologists generally consider scorekeeping as *the* mechanism of reciprocal altruism. The previous chapters examined whether bonding forms an alternative to the conventional scorekeeping mechanism, whether bonding is more biologically prepared than scorekeeping, and what is the role of emotions in scorekeeping and bonding behavior. In the concluding chapter I evaluate the answers to these questions, provided in the different chapters. Each of the following sections is devoted to one chapter. After a summary of the study, I conclude with assessing the degree to which the results support the idea that the bonding mechanism forms an alternative to the scorekeeping mechanism, or whether it provides support to the bonding mechanism being more prepared than the scorekeeping mechanism. Each section ends with suggestions for future research and a glance at recent developments. The final section of this chapter contains a general conclusion.

2 Evidence for bonding and scorekeeping behavior from anthropological studies on food sharing

2.1 Summary of study

When evolutionary psychologists argue for the importance of scorekeeping or cheater detection mechanisms, they often refer to food sharing practices in hunter-gatherer societies. Since hunter-gatherers live in conditions that are most similar to those of our ancestors, evidence for scorekeeping in those people would form a strong indication for the conventional idea that our ancestors have evolved a scorekeeping mechanism to cope with the risk of being cheated. In Chapter 2, I took a closer look at anthropological studies on food sharing to determine whether they supported a scorekeeping mechanism or whether the observed sharing practices could also be explained by a bonding mechanism.

Both more descriptive cultural anthropological studies and more quantitative evolutionary anthropological studies were scrutinized. Since neither of those traditions explicitly dealt with the question whether food sharing practices are the result of a bonding mechanism or a scorekeeping mechanism, hypotheses were derived that could be tested with the available data or were actually tested. The cultural anthropological studies were generally supportive to the hypotheses based on the bonding mechanism. Sharing patterns are egalitarian in small groups, and individuals who are in need of food receive food from their group members or friends. There was no strong support for the hypothesis that in larger groups, individuals restrict their sharing to a limited number of friends.

Hypotheses about scorekeeping reciprocity were mainly taken up by the evolutionary anthropological tradition. There was no evidence that individuals avoid to give to free-riders, avoid to be considered a free-rider, or exchange food for other commodities (e.g., sex). In contrast to this, several studies reported support to the most important hypothesis following from the scorekeeping mechanism, i.e., that giving is contingent upon receiving.

In the final section, however, I argued that these results do not provide convincing evidence to the scorekeeping mechanism for two reasons. First, most of these studies use relative measures of sharing. Since these measures control for a person's or household's total amount of food resources, they are confounded with *the ability to give*, and, as a consequence, with *need*. Second, to assess the relation between the total amount of food a person has received from another person, and the total amount he has provided to this person, all of these studies use correlational measures, or at best, regression analyses in which a limited number of variables are controlled for. However, a positive correlation between food received

and food provided does not necessarily imply that sharing behavior is governed by a concern with maintaining a balanced relationship. It can also be the result of individuals preferentially sharing food with a small group of friends in a non-contingent way. To determine whether people engage in contingent sharing, sequential data of food sharing practices are needed.

2.2 Main conclusions

Based on this review, the frequent references to anthropological studies on hunter-gatherer food sharing as illustrations of scorekeeping behavior can be questioned. The data are either supportive or empirically equivalent to the idea of a bonding mechanism. Therefore, based on the anthropological data, the bonding mechanism can indeed be considered an important alternative to the conventional scorekeeping mechanism.

2.3 Suggestions for future research and recent developments

The importance of using time-dependent measures to assess contingent sharing has also been acknowledged by anthropologists, but is difficult to implement because it requires a sufficiently large sample size and time duration (Gurven, in preparation). In a recent study, Gurven used a crude time-dependent estimate by splitting his sample into two time periods (of approximately one month each), and regressing the amount of food B received from A in the second time period on the amount of food A received from B in the first time period (Gurven, in preparation). Although contingency estimates of some of the resources types remained highly significant, they were much smaller than the conventional contingency estimates in which the total amount of food B received from A was regressed on the total amount of food A received from B. Therefore, it is doubtful whether contingency estimates would remain significant if less crude measures were used. Nevertheless, more studies using time-dependent measures are needed to settle the issue of whether sharing is contingent.

3 Successfulness of bonding and scorekeeping strategies in a simulation study

3.1 Summary

The central claim of Chapter 3 was that the popularity of the idea that reciprocal altruism is governed by a scorekeeping or cheater detection mechanism is the result of the use of the Prisoner's Dilemma game as the conventional way to study the evolution of reciprocal altruism. In the iterated Prisoner's Dilemma game, actors are *externally* assigned to each other and forced to make a move, that is: either cooperate or defect. Furthermore, the iterated game consists of a series of one-shot games, *in each of which both actors make a move*. Chapter 3 introduced an alternative model to study the evolution of reciprocal altruism: the Social Evolution Model (SEM). In contrast to the Prisoner's Dilemma game, the SEM allows actors to select their interaction partners themselves. This implies that actors are not only endowed with a strategy explicating the conditions under which to cooperate (or help), but also with a strategy explicating which other actor to *select* as an interaction partner. A second essential difference with the Prisoner's Dilemma is that nature is added as a player. In each round every actor has a *certain probability* to be hit by nature and get in distress, and consequently needs to find a helping partner. Given that evolutionary psychologists argue that our behavioral mechanisms have originated in the ancestral environment, which was characterized by highly unpredictable success rates of acquiring food, both of these characteristics make the SEM a better model to investigate the evolution of reciprocal altruism than the Prisoner's Dilemma game.

Through a series of simulations we investigated the relative success of two cooperative strategies, modeled in accordance to the bonding mechanisms and the scorekeeping mechanism, in invading and subsisting in a population of non-cooperative actors. The scorekeeping strategy (called Keeping Books Balanced) always acted in such a way as to minimize the difference between the number of times that help had been provided from an actor and the number of times that help had been received to this actor. Thus, when asked for help, Keeping Books Balanced actors only helped if the requester was not indebted to them, and preferred to help actors to whom they were indebted themselves. When in need of help, they preferred to be helped by actors who were indebted to them. In contrast, the bonding strategy (called Commitment) always returned to those actors who had proved to be helpful in previous interactions. Thus, both when asked for help and when in need for help, Commitment actors preferred to help or to receive help from those actors who had helped them most often.

In separate simulations, both strategies were confronted with actors following a non-cooperative strategy. Those non-cooperative actors asked for help when in need, but never to the same actor for a second time, and when asked for help they always refused. Simulations were run with different population sizes and various initial proportions of cooperative actors. Additional model parameters were the probability of getting in distress (harshness of conditions), and the costs of helping (operationalized as an increase in the probability of getting in distress in the next round). After 30 rounds the proportion of surviving cooperative actors was recorded as the ratio of the total number of survivors. If this proportion was larger than the initial proportion of cooperative actors, this was interpreted as an increase in cooperators in the next generation. If such an increase occurred at all initial proportions of cooperative actors, this was taken as an invasion by cooperative actors over the course of generations.

The results showed that in general, Commitment actors and Keeping Books Balanced actors were equally successful in *resisting* an invasion of non-cooperative actors. However, Commitment actors were more successful in *invading* a population of non-cooperative actors if conditions were harsh or if population sizes were medium-sized or large. In those conditions, the minimum number of actors that could achieve an invasion in a population of non-cooperative actors was lower for Commitment than for Keeping Books Balanced.

3.2 Main conclusions

The results of the simulations indicate that over the course of generations, a reciprocal altruistic strategy that is not primarily focused on avoiding to be exploited does not do worse than a strict scorekeeping strategy. Moreover, in those conditions that are most similar to those of the Pleistocene savanna (i.e., in conditions with the highest probability of getting in distress), the bonding strategy is even more successful than the scorekeeping strategy in invading a population of non-cooperative actors. Therefore, based on this simulation study the bonding mechanism can indeed be considered an important alternative mechanism of reciprocal altruism. Moreover, the results may be interpreted as suggesting that rather than to a scorekeeping mechanism, ancestral conditions gave rise to a bonding mechanism.

3.3 Suggestions for future research and recent developments

Although the simulation study focused on the relative success of two specific cooperative strategies, simulation researchers might raise the criticism that the inclusion of more different strategies - both cooperative and defecting - would have resulted in more robust conclusions. Furthermore, it is also unclear whether the same results would have been found if the model had incorporated noise, that is, the possibility of misperceiving another actor's behavior. Currently, new simulations are prepared with various cooperative strategies and various cheater strategies, including a strategy that does not keep scores in the sense of primarily acting on the difference between the number of times help has been provided and the number of times help has been received, but that *does* take note if the other actor has *refused* to grant a previous request for help (Back 2004). The results of these simulations may be highly relevant to understanding the difference between scorekeeping in the sense of retaliating another person's *indebtedness*, and a more literal translation of the Tit for Tat strategy - retaliating a *previous refusal* to a request for help (see Section 5.3.2).

In addition, the SEM has been extended to investigate the effects of generalized exchange, that is, of actors being able to select their helping partners based on information from third parties. Currently, simulations are being run with actors who provide information about their past interaction history if they are being asked for help while being unable to grant the request themselves (de Vos and Elsas, in preparation).

4 Evidence for bonding and scorekeeping behavior from dilemma situations

4.1 Summary of study

Chapter 4 followed up with the common distinction in the social science literature between communal and exchange relationships. We re-interpreted these two relationships types in terms of the bonding and the scorekeeping mechanism. Whereas the bonding mechanism is triggered by the cue "friend in need", the scorekeeping mechanism is activated by an imbalance in the amount of benefits provided and received. The main question of Chapter 4 was what happens when individuals are confronted with cues from both mechanisms, thus posing a dilemma between bonding and scorekeeping. Under what conditions will they

respond by providing help to a needy person, and under what conditions will they try to maintain a balanced relationship?

These questions were addressed through two scenario experiments, in which subjects had to indicate their responses to a number of dilemma situations. One scenario posed a dilemma between helping a needy person and reciprocating a creditor (*Reciprocate vs help dilemma*), a second scenario concerned a dilemma between helping and refusing a person who was in one's debt (*Debtor in need dilemma*), and a third one posed a dilemma between helping and refusing a person who himself had refused to help at a previous encounter (*Refuser in need dilemma*). Both the context of the helping situation (lending money versus providing assistance in the case of illness) and the relationship with the requester (good friend versus acquaintance) were varied between subjects.

In addition, the second study also included an attempt to assess whether one of the two mechanisms had a higher priority, or was more biologically prepared, than the other one. This was done by presenting subjects with an implicit prime in the form of a language correction task, concerning stories about either a typical bonding, a typical scorekeeping, or a neutral situation.

In line with expectations subjects were more likely to perform bonding behavior towards friends than towards acquaintances. Furthermore, in the illness context the degree of bonding responses was much higher than it was in the money context. The effects of the implicit prime were inconsistent and difficult to interpret.

4.2 Main conclusions

The scenario experiments show that different conditions elicit different responses on a dilemma between helping a needy one and avoiding an imbalanced relationship. Although there is no support that the bonding mechanism is more prepared than the scorekeeping mechanism, the results show that individuals do not keep scores of benefits provided and benefits received in all conditions. Moreover, the specific conditions that foster bonding behavior, i.e., the other being a friend and the other being ill and in need of assistance, are most similar to the living conditions and the adaptive problems of our ancestors. Therefore, Chapter 4 does demonstrate the importance of considering bonding as an alternative to the conventional scorekeeping mechanism.

4.3 Suggestions for future research and recent developments

4.3.1 Studying biological preparedness by implicit primes

Although the implicit prime manipulation failed in this study, it would be premature to discard it as a possible method of testing hypotheses about differences in biological preparedness. If highly prepared responses are more easily triggered by an implicit prime than less prepared responses, it might be a valuable method to test whether certain behavioral patterns are the result of evolved psychological mechanisms or whether they are primarily "cultural" patterns. However, before engaging in tests concerning complex mechanisms like scorekeeping and bonding, the implicit prime method should be calibrated using more straightforward mechanisms whose evolutionary status is no longer under debate. For example, one might follow up on Seligman's (1971) suggestions concerning differences in preparedness to learn specific kinds of fear responses. Starting with the assumption that fear responses to rats, spiders, or snakes are more prepared than fear responses to household objects or, let's say, lambs, one would expect that an implicit prime concerning a snake would evoke stronger fear responses on a mood scale, compared to an implicit prime concerning a lamb or a wooden block. When such preliminary studies show that responses whose biological preparedness is not under debate anymore, such as fear responses to snakes, are indeed triggered more easily by implicit primes than non-prepared responses, one can use this method to determine preparedness differences between psychological mechanisms.

In addition, both content and form of the implicit primes should be the subject of preliminary studies. Before presenting specific cues (e.g., stories, pictures, words) as implicit primes, their validity as scorekeeping or bonding cues should be ascertained.

4.3.2 The effect of relationship

Chapter 4 reported only a modest effect of relationship with Alter. However, many studies have found strong evidence for an effect of relationship on helping behavior or preferred distributions of resources. Compared to strangers, friends have been shown to be less concerned with maintaining a balanced relationship, and more concerned with responding to each others' needs (see Clark and Grote 2003). Recently, even non-human primates have been found to react differently to situational cues closely related to scorekeeping, dependent on the closeness of the relationship with their interaction partner. Brosnan and de Waal (2003; see also

Brosnan et al., in press) conducted experiments among capuchin monkeys and chimpanzees that were based on Ultimatum and Dictator Games used in behavioral economics (e.g., Fehr and Schmidt 2003). Pairs of subjects were taught to exchange tokens for food rewards with a human experimenter. It was found that subjects responded negatively to unequal distributions. Thus, they often refused to exchange, or rejected the reward, when their partner received a better reward, an effect which was amplified if the partner received the better reward without needing to hand over the token. The chimpanzee experiments also considered the effect of relational variables. Dominance rank did not have any effect, but relationship closeness did. Pairs of chimpanzees who had been co-housed in the same group for a long time were less likely to reject unequal distributions than pairs who were co-housed for a shorter time.

The results of these experiments, suggesting that non-human primates do not like underbenefiting compared to a co-specific, seem to contradict the hypothesis that scorekeeping is a recent cultural adaptation to market society.[1] At the same time, however, they also question the ubiquity of the scorekeeping mechanism. Thus, the authors conclude that "tolerance of inequity may increase with social closeness between partners, such as friends and family, in a wide variety of species, a hypothesis that deserves further testing in both humans and non-human primates." (Brosnan et al., in press, p. 11)

A planned collaborative study with some of the authors elaborates on the effect of relationship on inequity aversion among human subjects. This study will not only re-examine the effect of social closeness, but also focus on the effect of another basic relationship type: one between two individuals of different status. An interesting hypotheses is that high status individuals are more interested in (and more capable) to boast their status by "generously" giving up resources at the benefit of lower status individuals, resulting in a preference for underbenefiting, both to overbenefiting and a balanced relationship. The focus on different types of relationship may increase our knowledge about the conditions favoring different mechanisms of reciprocal altruism.

[1] In defense of this hypothesis, it should be mentioned that the exchanges did not occur "spontaneously" but required explicit training, that the reported results of the capuchin experiment only concerned five female subjects since pretests had shown that males did not react to inequity (Brosnan and de Waal 2003), and that neither of the studies provided support to the other component of scorekeeping behavior, avoidance of overbenefiting.

5 Emotions associated with bonding and scorekeeping behavior

5.1 Summary of study

The scenario experiments discussed in Chapter 4 also contained measures of emotional responses. Chapter 5 focused on the emotion responses obtained in one of those experiments. In contrast to the previous chapters, this study was not so much concerned with the question whether or under what conditions individuals behave according to the bonding or the scorekeeping mechanism. Rather, the two mechanisms were considered as given, and used to derive hypotheses about the relation between emotions and behavioral responses. Based on the scorekeeping mechanism, it was hypothesized that refusing to help a requester who is in one's debt or who has refused to help at a previous encounter is instigated by Retaliatory emotions like indignation and anger. Similarly, reciprocating someone to whom one is indebted was predicted to be the effect of Urge-to-Reciprocate emotions like guilt, obligation, gratitude and fear of retaliation. Based on the bonding mechanism, we predicted that helping a needy person is the result of Bonding emotions like commitment and warmth.

In addition to relations between specific emotions and behavioral responses, we also tested the general evolutionary psychological assumption that emotions form the link between cues and behavior. This was done by examining the degree to which the emotion variables mediated the effect of situational variables (e.g., object of help and relationship with the requester) on behavioral responses. We also predicted that emotions would mediate the effect of personality variables on behavioral responses.

Logistic regression analyses confirmed the relation between Bonding emotions and helping behavior, as well as the relation between Retaliatory emotions and refusing to help a debtor or refuser. There was less support for the effect of Urge-to-Reciprocate emotions. Only subjects who were highly sensitive to injustice showed the expected relation between guilt and reciprocating behavior. Moreover, only in the case of money did obligation lead to reciprocating behavior. Gratitude and fear of retaliation did not have any effect on behavioral response.

The intermediating role of emotions was supported for the dilemma between helping and refusing a debtor or refuser. In contrast, in the dilemma between helping a needy one and reciprocating a creditor, there was no support for a mediating role of emotions between situational and personality characteristics on the one hand, and behavior response on the other hand. Rather, they seem to play a moderating role.

5.2 Main conclusions

Chapter 5 did not involve a confrontation of the scorekeeping and the bonding mechanism, but considered both as given. Therefore, it does not provide a test concerning the biological primacy of either mechanism. However, the results of Chapter 5 do demonstrate that individuals' responses on requests for help are not only affected by typical scorekeeping emotions like anger and indignation, but also by emotions expressing a bond to the other person and a concern for his well-being. Furthermore, Chapter 5 provided partial support to the evolutionary psychological interpretation of emotions, namely as forming the link between cues from the environment and personality characteristics on the one hand, and behavioral responses on the other hand.

5.3 Suggestions for future research

5.3.1 Effect of specific emotions

Chapter 5 provided support to the importance of Bonding emotions, like commitment and warmth, for helping behavior, as well as the importance of Retaliatory emotions, like anger and indignation, for avoiding underbenefiting. In contrast, the role of the alleged Urge-to-Reciprocate emotions, like gratitude, obligation and fear of retaliation, is unclear. As was suggested, this might be due to the fact that these emotions concern secondary emotions and are more liable to differences in interpretation. However, it is also possible that these emotions have different functions than the ones hypothesized. For example, rather than functioning as an incentive to directly return a favor, the emotion of gratitude might simply function to strengthen one's bond with a benefactor. More studies on the functions of specific emotions are needed to solve these issues.

5.3.2 Indebtedness versus refusals

A number of findings of both Chapter 4 and Chapter 5 suggested that we may need to qualify the scorekeeping mechanism. In both chapters, avoiding underbenefiting was operationalized in two ways. In the *Debtor in need dilemma* it was operationalized as avoiding Alter to be in my debt. In the *Refuser in need dilemma*, a more literal translation of the Tit for Tat strategy was followed, with avoiding underbenefiting being operationalized as avoiding to provide help to Alter if he refused to help me at a previous encounter.

Although the general pattern in behavioral and emotional responses was more or less similar, subjects reacted much more negatively to a requester who had refused to help them at a previous encounter than they did to a requester who was in their debt. This was especially the case in the illness context, where subjects were less likely to grant a request for help, reported less Bonding emotions and Obligation and more Retaliatory emotions, needed to be relatively prosocial to grant the request, and needed to have a relatively close relationship with the other person to grant the request. These results may be interpreted as pointing to the importance of responding to each other's needs. Although people do not mind if someone is indebted to them, they do mind if someone refused to help them when they were in need.

Future research should shed more light on the differences between these two types of relationship imbalances. The reported results suggest that people are more likely to forgive debts than to forgive refusals. Moreover, one might speculate that friendship dissolution is not the result of me giving more benefits to my friend than he returns to me, but of my friend letting me down when I need his help.

6 General conclusion

After reviewing the four chapters, can we conclude that the attempt to establish bonding as an alternative to the conventional scorekeeping mechanism of reciprocal altruism has succeeded? I think we can. Food sharing practices by hunter-gatherers, which are often used as an illustration of scorekeeping, were demonstrated either to explicitly support or to be empirically equivalent to a bonding mechanism. Furthermore, compared to a scorekeeping strategy, bonding proved to be an equally or even more successful strategy when confronted with a non-cooperative strategy in a simulated environment characterized by a high probability of getting in distress. Moreover, when confronted with a dilemma between bonding and scorekeeping behavior, many subjects responded in accordance with the bonding mechanism, especially in conditions that were most similar to the ancestral environment. Finally, typical bonding emotions like commitment and warmth were shown to have a significant effect on reciprocal altruistic behavior.

Can we also draw conclusions about the biological primacy of one either mechanisms? In Chapter 1, I speculated that the bonding mechanism might be more biologically prepared than the scorekeeping mechanism. According to this

idea, the bonding mechanism has evolved far back in our evolutionary past, whereas scorekeeping is a relatively recent cultural adaptation. As a consequence, bonding behavior is learnt and triggered very easily, whereas it takes more effort to learn and to perform scorekeeping behavior (cf. de Vos 2004; de Vos and Wielers 2003; Hoyt 1926; Tooby and Cosmides 1996). Did the previous chapters provide any evidence to the evolutionary primacy of one of either mechanisms? The simulation study provided some support to the claim that the bonding mechanism is more likely to have been selected for in the ancestral environment than the scorekeeping mechanism is. The only empirical test of the hypothesis about differences in preparedness concerned a comparison of behavioral responses between subjects who were confronted with implicit primes for either scorekeeping or bonding behavior. This test did not give a definite answer.

In sum, although this dissertation has demonstrated that the scorekeeping mechanism is not so ubiquitous as is generally believed, many questions still have to be answered. More research is needed to determine what are the relevant cues for bonding and scorekeeping, what are the conditions in which the bonding and scorekeeping mechanism are operational, and what emotions are associated with either bonding or scorekeeping behavior. And finally, the issue of whether one of either mechanisms is more biologically prepared than the other, and how to determine differences in biological preparedness in general, needs both theoretical and empirical elaboration.

APPENDIX 1: Scenarios (Chapters 4 and 5)[1]

Debtor in need dilemma - Money context

D. is a good friend/ acquaintance of yours. One night there is a message on your voicemail from D.

D. says that his/her purse has been stolen, even though he/she is always careful with his/her things. He/she needs € 100,- to do some urgent shopping. D. asks you to lend him/her € 100,-.

D. knows few other persons whom he/she can appeal to. You just received your salary, so you can afford to miss € 100,-, but not more than that amount.

Recently however, D. borrowed a considerable amount of money from you because his/her laundry machine suddenly needed repairs. D. has not repaid you since then.

Assume that D. and you have about the same income.

Debtor in need dilemma - Illness context

D. is a good friend/ acquaintance of yours. One night there is a message on your voicemail from D.

D. says that he/she has attracted the flu. He/she asks you to come over and take care of him/her the next day.

D. knows few other persons whom he/she can appeal to. You have some spare time the next day, but not very much.

However, recently you have already taken care of D. when he/she was ill.

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[1] Translated from Dutch.

Refuser in need dilemma - Money context

R. is a good friend/ acquaintance of yours. One night there is a message on your voicemail from R.

R. says that his/her purse has been stolen, even though he/she is always careful with his/her things. He/she needs € 100,- to do some urgent shopping. R. asks you to lend him/her € 100,-.

R. knows few other persons whom he/she can appeal to. You just received your salary, so you can afford to miss € 100,-, but not more than that amount.

Recently however, you had a similar problem because you had lost you purse. You asked R. to lend you € 100,-, but R. answered that he/she did not have so much money available. You were quite certain, however, that R. could have missed it.

Assume that R. and you have about the same income.

Refuser in need dilemma - Illness context

R. is a good friend/ acquaintance of yours. One night there is a message on your voicemail from R.

R. says that he/she has attracted the flu. He/she asks you to come over and take care of him/her the next day.

R. knows few other persons whom he/she can appeal to. You have some spare time the next day, but not very much.

However, recently you were ill yourself. You asked R. to come over and take care of you then, but R. answered that he/she lacked the time. You were quite certain, however, that R. could have made some time for you.

Repay vs help dilemma - Money context

C. en N. are two good friends/ acquaintances whom you have known for about the same time. One night there are two messages on your voicemail: one from C. and one from N.

C. wants to buy knew clothes the next day, but he/she lacks the money. Recently you needed € 100,- to repair your bike. You asked C. to lend you € 100,-, which he/she did. C. asks you if you can repay him.

N. says that his/her purse has been stolen, even though he/she is always careful with his/her things. He/she needs € 100,- to do some urgent shopping. N. asks you to lend him/her € 100,-.

Both C. and N. know few other persons whom they can appeal to. You just received your salary, so you can afford to miss € 100,-, but not more than that amount.

Assume that C. and N. do not know each other and that all of you have about the same income.

Repay vs help dilemma - Illness context

The flu is reigning. C. en N. are two good friends/ acquaintances whom you have known for about the same time. One night there are two messages on your voicemail: one from C. and one from N.

C. has a touch of flu and asks you to come over and take care of him/her the next day. Recently you had a touch of flu yourself. You asked C. to come over and take care of you, then, which he/she did.

N. too has the flu, but a more serious variety which prevents him/her from leaving the house. Also N. asks you to come over and take care of him/her the following day.

Both C. and N. know few other persons whom they can appeal to. You have some spare time the next day, but not enough to help the both of them.

Assume that C. and N. don't know each other.

APPENDIX 2: Mean behavioral response, sd, and N for the three dilemmas, according to experimental condition. (Chapter 4, Study 2)

Context	Relationship with Alter	Prime	*Reciprocate vs help*		*Debtor in need*		*Refuser in need*		Dilemma (compound measure)		N
			M	sd	M	sd	M	sd	M	SE	
Money	Friend	Bond	2.00	.95	2.60	.72	2.33	.71	2.31	.09	30
		Score	2.19	.88	2.37	.84	2.26	.86	2.27	.09	27
		Neu	2.33	.88	2.89	.89	2.70	.61	2.64	.09	27
		total	2.17	.90	2.62	.83	2.43	.75	2.41	.05	84
	Acquaintance	Bond	2.19	1.1	2.35	.61	2.19	.95	2.25	.09	31
		Score	2.18	.86	2.36	.73	2.46	.69	2.33	.09	28
		Neu	2.17	.87	2.40	.72	2.13	.82	2.23	.09	30
		total	2.18	.92	2.37	.68	2.26	.83	2.27	.05	89
	Total		2.17	.91	2.49	.77	2.34	.80	2.34	.04	173
Illness	Friend	Bond	3.00	.65	3.41	.56	2.85	.56	3.09	.08	34
		Score	3.19	.49	3.42	.64	2.88	.86	3.17	.09	26
		Neu	3.09	.63	3.52	.51	3.00	.75	3.20	.08	33
		total	3.09	.60	3.45	.56	2.91	.72	3.15	.05	93
	Acquaintance	Bond	3.15	.60	3.37	.56	2.63	.69	3.05	.09	27
		Score	2.80	.89	3.37	.56	2.40	.67	2.86	.09	30
		Neu	3.13	.68	3.70	.47	2.77	.68	3.20	.09	30
		total	3.02	.75	3.48	.55	2.60	.69	3.04	.05	87
	Total		3.06	.67	3.47	.55	2.76	.72	3.09	.04	180
Total	Friend		2.65	.89	3.06	.82	2.68	.77	2.78	.04	177
	Acquantance		2.60	.94	2.92	.83	2.43	.78	2.65	.04	176
Total		Bond	2.58	.96	2.93	.77	2.51	.77	2.67	.04	122
		Score	2.59	.90	2.88	.86	2.50	.77	2.66	.05	111
		Neu	2.70	.88	3.14	.83	2.66	.78	2.82	.04	120
Total all			2.62	.91	2.99	.83	2.56	.79	2.72	.03	353

Note: Behavioral response was measured on a 4-point scale, with 1=definitely scorekeeping and 4=definitely bonding.

APPENDIX 3: Results of seven Principal Factoranalyses and Reliability analyses on the emotion variables (Chapter 5)

	Avoiding overbenefiting vs helping			Avoiding underbenefiting vs helping	
	Needy one	Creditor	Expected if refuse	Debtor/ Refuser	Expected if refuse
Factor loadings					
Contempt	.76	.74	.75	.64	.67
Anger	.75	.48	.81	.76	.77
Disappointment	.74	.87	.82	.80	.76
Indignation	.62	.62	.83	.78	.71
Irritation	.61	.67	.80	.79	.74
Commitment	.81	.77		.60	.69
Warmth	.70	.62	.67	.52	.88
Gratitude	.39	.45 #	.32 #	.50	.23 #
Worriedness	.44	.50	.33 #	.45	
Obligation		.77	.50	.63	.80
Guilt	.52 #	.37		.49	.67
Number of extracted factors	3	3	3	2	3
Alphas					
Retaliatory emotions	.80	.78	.90	.87	.85
Bonding emotions	.73	.67		.75	

Notes: Factor extraction based on Eigenvalue>1 and Oblimin rotation. Factor loadings from Pattern matrix. For each emotion only the highest factor loading is displayed. Dashed lines indicate borders between factors.
Double loadings (difference between absolute loadings <.10) and factor loadings smaller than .20 are not shown.
= Low communality of extracted factor solution (H^2 <0.20).

APPENDIX 4: Frequency distributions of emotion and behavioral responses in the three dilemmas (Chapter 5)

		Reciprocate vs help dilemma		Debtor in need dilemma	Refuser in need dilemma
		Emotion towards N	Emotion towards C		
Bonding emotions[1]	Not at all	3.4	3.1	11.0	26.3
	Little	32.2	27.4	50.9	59.2
	Quite	51.4	55.8	32.0	13.5
	Strong	12.9	13.8	6.0	1.0
	N	100(379)	100(384)	100(381)	100(377)
Worriedness	Not at all	3.6	45.5	6.8	27.9
	Little	29.1	34.1	46.5	56.0
	Quite	49.1	18.1	41.5	14.6
	Strong	18.2	2.3	5.2	1.6
	N	100(385)	100(387)	100(383)	100(384)
Retaliatory emotions[1]	Not at all	93.3	95.5	50.3	10.4
	Little	5.7	4.0	40.6	54.9
	Quite	1.1	0.6	8.0	32.6
	Strong	0.0	0.0	1.1	2.1
	N	100(378)	100(377)	100(379)	100(375)
Obligation	Not at all	14.2	3.4	25.1	54.9
	Little	42.0	18.8	43.1	34.9
	Quite	30.7	48.4	25.6	10.0
	Strong	13.1	29.4	6.3	0.3
	N	100(381)	100(384)	100(383)	100(381)
Guilt	Not at all	52.7	22.6	66.5	80.4
	Little	32.6	44.7	25.1	17.3
	Quite	12.5	25.7	7.6	2.4
	Strong	2.1	7.0	0.8	0.0
	N	100(383)	100(385)	100(382)	100(382)
Gratitude	Not at all	79.0	19.7	81.5	95.0
	Little	18.4	27.2	11.7	4.4
	Quite	2.3	43.0	5.5	0.3
	Strong	0.3	10.1	1.3	0.3
	N	100(385)	100(386)	100(384)	100(383)

(Appendix 4 continued)

		Reciprocate vs help dilemma		Debtor in need dilemma	Refuser in need dilemma
		Emotion towards N	Emotion towards C		
Expected Retaliatory emotions[1]	Not at all	11.9 [2]		10.3	12.7
	Little	55.6 [2]		54.1	62.3
	Quite	27.0 [2]		31.3	23.0
	Strong	5.7 [2]		4.4	2.1
	N	100(355)		100(368)	100(370)
Behavioral response	Definitely not helping	14.2		4.2	9.5
	Probably not helping	23.9		21.3	31.7
	Probably helping	46.4		46.2	50.9
	Definitely helping	15.5		28.3	7.9
	N	100(373)		100(381)	100(379)

Notes:

[1] Percentages are based on summation scores of the relevant emotion items, rounded to the four categories

[2] In the *Reciprocate vs help dilemma*, Expected Retaliatory emotions were only measured towards the requester who was chosen to help

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SAMENVATTING

‘Voor wat hoort wat’ versus ‘Heb uw naaste lief’. Twee proximate mechanismen voor wederkerig altruisme

Inleiding

Stelt u zich voor dat een goede vriend buiten zijn schuld in financiële problemen zit, bijvoorbeeld omdat zijn portemonnee is gestolen. Wat zou u doen als hij u vroeg om hem wat geld te lenen? Vooropgesteld dat uw banksaldo het toestond zou u zijn verzoek waarschijnlijk wel inwilligen. Maar hoe zou u reageren als hij een paar dagen later weer bij u kwam met de vraag om hem een lift te geven naar het politiebureau om de diefstal aan te geven? En wat als hij u drie weken later om een nieuwe lening vroeg omdat hij nog steeds problemen had om toegang te krijgen tot zijn bankrekening? Waarschijnlijk zou u heen en weer geslingerd worden tussen twee overwegingen: Aan de ene kant irritatie en verontwaardiging vanwege het zoveelste verzoek om een gunst waardoor de vriendschap uit balans dreigt te raken. Maar aan de andere kant horen vrienden elkaar te helpen als ze hulp nodig hebben. U lijkt te moeten kiezen tussen de uitdrukking “voor wat, hoort wat” en “heb uw naaste lief”.

Deze twee overwegingen vormden het onderwerp van dit proefschrift. Vanuit een evolutionair psychologisch perspectief kunnen zij beschouwd worden als programma’s in onze hersenen die ontstaan zijn om de specifieke problemen die onze voorouders tegenkwamen het hoofd te bieden. Zulke programma’s

worden *proximate mechanismen* genoemd omdat ze een antwoord geven op de vraag hoe mensen zich gedragen onder bepaalde condities. Evolutionair psychologen benaderen deze vraag door zich af te vragen wat de *ultimate oorzaken* van bepaalde gedragsmechanismen zijn; dat wil zeggen: ze zijn geïnteresseerd in de baten van het betreffende gedrag voor het overleven en de voortplanting van het individu dat dit gedrag vertoont (fitness). De ultimate oorzaken van het geven van hulp of het verlenen van een dienst aan iemand die geen familie is, komen neer op *wederkerig altruïsme*: het helpen van iemand anders levert baten op als deze persoon die hulp in de toekomst reciproceert.

De meeste evolutionair psychologen denken dat wederkerig altruïsme via een "voor wat hoort wat" of *scorekeeping* mechanisme verloopt. Dit mechanisme zorgt ervoor dat wij (onbewust) bijhouden hoeveel we van iemand ontvangen hebben en hoeveel we hem gegeven hebben, en proberen te vermijden dat die balans verstoord raakt. De reden is dat iemand die hulp aanneemt maar nooit iets terugdoet een hogere fitness heeft dan iemand die iedereen helpt.

Een aantal argumenten pleit echter tegen het idee dat scorekeeping het primaire mechanisme voor wederkerig altruïsme is. Ten eerste lijken interacties tussen vrienden, die bij uitstek een relatie hebben waarin sprake is van elkaar helpen of een plezier doen, allerminst gekenmerkt te worden door scorekeeping, maar veeleer door non-instrumentele bezorgdheid om elkaars welzijn en de bereidheid om elkaar te helpen als dat nodig is. Ten tweede is het zeer twijfelachtig of een scorekeeping mechanisme wel zo gunstig was in de omgeving waarin onze voorouders leefden. Aangezien de savanne werd gekenmerkt door zware en onvoorspelbare omstandigheden - voedsel was moeilijk te vinden en overal loerden roofdieren – zou het bijhouden van ontvangen en gegeven hulp juist contraproductief kunnen werken. Door iemand hulp te ontzeggen omdat hij in je schuld stond, liep je de kans om een waardevol groepslid te verliezen.

Op grond van deze en andere argumenten lijkt een mechanisme dat primair gericht is op het welzijn van de personen in iemands nabije omgeving, een "heb uw naaste lief" of *bonding* mechanisme - een serieus alternatief te vormen voor scorekeeping als proximaat mechanisme voor wederkerig altruïsme.

Dit proefschrift richtte zich op de vraag in hoeverre het bonding mechanisme een alternatief vormt voor het conventionele scorekeeping mechanisme. Op een aantal plaatsen werd een stap verder gegaan en onderzocht ik de hypothese dat het bonding mechanisme biologisch meer primair is, terwijl het scorekeeping mechanisme een relatief recente culturele aanpassing is. Ten slotte werd de vraag gesteld naar de rol van emoties in beide mechanismen.

Bewijs voor bonding en scorekeeping vanuit antropologische studies naar het delen van voedsel

Meer dan in welke andere soort samenleving leven jagers-en verzamelaars in omstandigheden die lijken op die van onze voorouders. De aanwezigheid van scorekeeping of bonding gedrag in zulke samenlevingen zou dus een sterke aanwijzing vormen voor een vroege evolutionaire oorsprong van het ene dan wel het andere mechanisme. Evolutionair psychologen verwijzen vaak naar het delen van voedsel in jagers-en verzamelaarssamenlevingen als bewijs voor scorekeeping gedrag. Een kritische bespreking van de beschikbare empirische bevindingen ontbrak echter. In hoofdstuk 2 werd daarom een groot aantal antropologische studies over het delen van voedsel onder de loep gelegd om te bepalen of gevallen van het delen van voedsel beter door een scorekeeping of een bonding mechanisme kunnen worden beschreven.

De meer kwalitatieve *cultureel antropologische studies* leverden over het algemeen steun aan het bonding mechanisme. In overeenstemming met wat men zou verwachten op grond van het bonding mechanisme bleek er veel egalitair delen in kleine groepen voor te komen, evenals delen op basis van noden. Er waren geen aanwijzingen dat individuen in grotere groepen het delen van voedsel beperken tot een klein aantal "vrienden". Hoewel de meer kwantitatieve *evolutionair antropologische studies* expliciet gericht waren op het aantonen van scorekeeping gedrag, was de empirische evidentie zwak. De belangrijkste bevinding die voor scorekeeping leek te pleiten was de aanwezigheid van een positieve correlatie tussen hoeveelheid ontvangen voedsel en hoeveelheid gegeven voedsel. Een dergelijke interpretatie is echter vatbaar voor kritiek. Ten eerste maken de meeste studies die een positieve correlatie rapporteren gebruik van relatieve maten, die controleren voor de totale hoeveelheid voedsel van een persoon of huishouden, en daarmee voor de mate waarin men *in staat is* om te geven. Een dergelijke maat is verstrengeld met de *noden* van een persoon of huishouden en vormt dus geen eenduidige toets van scorekeeping gedrag. Ten tweede betekent een correlatie tussen de totale hoeveelheid die je ontvangen hebt van iemand en de totale hoeveelheid die je aan diegene gegeven hebt niet noodzakelijk dat mensen het geven van voedsel afstemmen op de hoeveelheid die zij van anderen ontvangen hebben. Een positieve correlatie kan ook het gevolg zijn van een patroon waarbij mensen binnen een kleine groep "vrienden" delen op basis van noden.

Samenvattend blijkt dat de antropologische studies over het delen van voedsel geen onomstotelijk bewijs leveren dat er een scorekeeping mechanisme aan

werd geïnterpreteerd als een aanwijzing dat in omstandigheden die het meest lijken op de omgeving waarin onze voorouders zich ontwikkelden (de savanne), een bonding strategie meer kans heeft om zich in de loop der generaties te verspreiden dan een scorekeeping strategie.

Scorekeeping en bonding gedrag in dilemmasituaties

Veronderstellend dat het scorekeeping mechanisme wordt geactiveerd door een *onbalans in de hoeveelheid hulp die men heeft ontvangen en de hoeveelheid hulp die men heeft gegeven* en het bonding mechanisme door de aanwezigheid van *een vriend die hulp nodig heeft,* rijst de vraag hoe mensen zich gedragen als ze geconfronteerd worden met "cues" die *beide* mechanismen activeren. Onder welke omstandigheden vinden ze het belangrijker om een hulpbehoevende bekende te helpen en onder welke omstandigheden geven ze de voorkeur aan het in balans brengen van de relatie?

Hoofdstuk 4 probeerde deze vraag te beantwoorden. In twee studies werden proefpersonen in totaal drie scenario's met dilemmasituaties voorgelegd. Eén scenario betrof een dilemma tussen het helpen van een hulpbehoevende bekende en het bewijzen van een wederdienst aan iemand bij wie de proefpersoon in de schuld stond (Helpen vs terugbetalen). Een tweede scenario beschreef een dilemma tussen hulp geven of weigeren hulp te geven aan een hulpbehoevende bekende die bij de proefpersoon in de schuld stond (Schuldenaar in nood). En een derde scenario betrof een dilemma tussen hulp geven of weigeren hulp te geven aan een bekende die eerder had geweigerd om de proefpersoon te helpen toen deze in nood was (Weigeraar in nood). Zowel de inhoud van de hulpdienst (geld lenen versus helpen bij ziekte) als de relatie met de andere persoon (vriend versus kennis) werden tussen proefpersonen gevarieerd. Bovendien bevatte één van de studies een impliciete stimulus. Het idee was dat het biologisch meest primaire mechanisme sterker zou worden geactiveerd door een dergelijke impliciete stimulus. Via een verhaaltje dat de proefpersonen vooraf moesten lezen en ontdoen van schrijffouten werd beoogd om ofwel het bonding mechanisme ofwel het scorekeeping mechanisme onbewust te activeren. Om het bonding mechanisme te activeren werd een tekst gebruikt over het belang van het helpen van vrienden; in geval van het scorekeeping mechanisme betrof het een tekst over de risico's van een ongebalanceerde relatie. In een derde conditie kregen proefpersonen een "neutrale" tekst te lezen.

In overeenstemming met de verwachting waren proefpersonen meer geneigd tot bonding gedrag ten aanzien van vrienden dan ten aanzien van

het werk is. De data pleitten ofwel vóór, of waren empirisch equivalent met het idee dat mensen delen op grond van een bonding mechanisme.

Het relatieve succes van een bonding strategie en een scorekeeping strategie in een simulatiestudie

Simulatiestudies naar de evolutie van wederkerig altruïstische of coöperatieve strategieën maken over het algemeen gebruik van modellen gebaseerd op het Prisoner's Dilemma. Deze modellen worden erdoor gekenmerkt dat actoren tegenover elkaar worden geplaatst en elke ronde de keuze hebben tussen twee gedragsopties: coöperen of defecteren. In zo'n voorspelbare omgeving vormt scorekeeping een logische strategie. Het centrale punt van hoofdstuk 3 was dat de populariteit van het scorekeeping mechanisme het gevolg is van het gebruik van het Prisoner's Dilemma voor het modelleren van de evolutie van wederkerig altruïsme.

In hoofdstuk 3 werd een alternatief model voor de evolutie van wederkerig altruïsme geïntroduceerd: het Sociale Evolutie Model (SEM). In tegenstelling tot het Prisoner's Dilemma model kiezen actoren in het SEM zelf hun interactiepartners. Daardoor is het gedragsrepertoire van actoren niet beperkt tot algoritmen die voorschrijven onder welke condities ze coöperen (helpen) of defecteren (niet helpen), maar ook algoritmen die voorschrijven hoe ze hun interactiepartners kiezen. Bovendien is er een onvoorspelbaarheidsfactor ingebouwd: in elke ronde heeft elke actor een bepaalde kans om in nood te raken en op zoek te moeten naar een interactiepartner die bereid is hem te helpen. Beide eigenschappen maken het SEM tot een meer realistisch model voor de evolutie van strategieën voor wederkerig altruïsme dan het Prisoner's Dilemma.

Door middel van een aantal simulaties werd van twee strategieën, gebaseerd op respectievelijk het scorekeeping mechanisme en het bonding mechanisme, onderzocht hoe succesvol ze waren in de loop der generaties. Voor beide strategieën werd gekeken in hoeverre actoren die zich gedroegen volgens de betreffende strategie, zich konden handhaven als ze werden geconfronteerd met actoren die wel hulp accepteerden maar nooit hulp gaven (niet-coöperatieven). Uit de resultaten bleek dat de bonding actoren over het algemeen even succesvol waren als de scorekeeping actoren. Onder bepaalde condities waren de bonding actoren echter succesvoller: als de kans om in nood te raken groot was, volstond een aantal van twee bonding actoren om een populatie van niet-coöperatieven binnen te dringen. Dit was bij de scorekeeping actoren niet het geval. Dit resultaat

kennissen. Daarnaast lokte ziekte veel meer bonding gedrag uit dan geldproblemen. Het effect van de impliciete stimulus was grillig en slecht interpreteerbaar.

De belangrijkste conclusie die op grond van deze resultaten getrokken kan worden, is dat - hoewel niet aangetoond kon worden dat het bonding mechanisme biologisch meer primair is dan het scorekeeping mechanisme - er tenminste bleek dat proefpersonen onder bepaalde omstandigheden geen scorekeeping maar bonding gedrag vertonen. Dit waren bovendien die omstandigheden die het meest leken op de condities waarin onze voorouders leefden.

De rol van emoties in scorekeeping en bonding mechanismen

Emoties spelen een belangrijke rol in de evolutionair psychologische opvatting over proximate mechanismen. Volgens deze opvatting vormen specifieke emoties de verbinding tussen enerzijds de "cues" die samengaan met de specifieke problemen die onze voorouders tegenkwamen en anderzijds de gedragsresponsen die onder die omstandigheden gunstig waren. In een van de studies uit hoofdstuk 4 was respondenten ook gevraagd naar emoties. Deze werden in hoofdstuk 5 geanalyseerd.

Ten eerste werd onderzocht welke emoties gepaard gaan met bonding gedrag en welke emoties gepaard gaan met scorekeeping gedrag. Op grond van het bonding mechanisme werd voorspeld dat *het helpen van een hulpbehoevende bekende* wordt gevoed door emoties als warmte en verbondenheid ("bonding emoties"). Op grond van het scorekeeping mechanisme werd voorspeld dat het *bewijzen van een wederdienst* aan iemand bij wie men in de schuld staat wordt ingegeven door emoties als dankbaarheid, verplichting en schuldgevoel ("wederdienst emoties") en de verwachting dat de ander boos zal zijn als de schuld niet vereffend wordt. Ook op basis van het scorekeeping mechanisme werd voorspeld dat het *afwijzen van een verzoek om hulp* door iemand die bij je in het krijt staat het gevolg is van emoties als verontwaardiging, irritatie en boosheid ("vergeldingsemoties").

Ten tweede werd de evolutionair psychologische assumptie getoetst dat emoties de verbinding tussen "cues" en gedragsresponsen vormen. Dit werd gedaan door te bepalen in hoeverre de emoties het effect van situationele variabelen (de inhoud van de hulpdienst en de relatie met de ander) op gedragsresponsen *mediëren*. Naast situationele variabelen werd ook naar het effect van een aantal persoonlijkheidsvariabelen gekeken.

De resultaten lieten zien dat er inderdaad een relatie was tussen bonding emoties en het helpen van een hulpbehoevende bekende. Eveneens kon worden

vastgesteld dat vergeldingsemoties gerelateerd zijn aan het afwijzen van een verzoek om hulp door iemand die bij je in het krijt staat. Er was minder steun voor het effect van wederdienst emoties. Alleen bij proefpersonen die in hoge mate gevoelig waren voor een onrechtvaardige behandeling vonden we de voorspelde relatie tussen *schuldgevoel* en het bewijzen van een wederdienst. En alleen in het geval van het lenen van geld leidde *verplichting* tot het bewijzen van een wederdienst. Dankbaarheid en de verwachting van vergeldingsemoties bij de ander bleken geen effect te hebben.

Tenslotte werd de mediërende rol van emoties alleen aangetoond voor de dilemma's tussen het helpen van een schuldenaar of weigeraar versus het afwijzen van diens verzoek om hulp. In het dilemma tussen het helpen van een hulpbehoevende bekende en het bewijzen van een wederdienst aan iemand bij wie men in het krijt staat bleken emoties veeleer een moderende dan een mediërende rol te spelen.

Conclusie

Op grond van de vier studies werd geconcludeerd dat het bonding mechanisme inderdaad als een alternatief voor het conventionele scorekeeping mechanisme beschouwd kan worden. Ten eerste bleek het delen van voedsel onder jagers-en verzamelaars net zo goed of beter door een bonding mechanisme te kunnen worden beschreven als door een scorekeeping mechanisme. Ten tweede bleek via simulaties met een niet-coöperatieve strategie dat de bonding strategie even succesvol was, en onder zware omstandigheden zelfs succesvoller, dan een scorekeeping strategie. Ten derde gedroegen proefpersonen die dilemmasituaties voorgelegd kregen tussen het helpen van een hulpbehoevende bekende en het in balans brengen van een relatie waarin de balans verstoord was, zich wel degelijk volgens het bonding mechanisme, vooral onder condities die het meest de levensomstandigheden van onze voorouders benaderden. En tenslotte oefenden typische bonding emoties als verbondenheid en warmte een belangrijke invloed uit op wederkerig altruïstisch gedrag.

De vraag of het bonding mechanisme meer biologisch primair is dan het scorekeeping mechanisme kon op grond van de hier gerapporteerde resultaten niet bevestigend worden beantwoord. De resultaten van de simulatiestudie zouden kunnen worden geïnterpreteerd als aanwijzing dat de levensomstandigheden van onze voorouders eerder aanleiding gaven tot de evolutie van een bonding mechanisme dan tot de evolutie van een scorekeeping mechanisme. De enige

expliciete toets van de betreffende hypothese gaf geen uitsluitsel: uit de resultaten bleek niet dat een impliciete stimulus voor bonding meer effect heeft op het gedrag van proefpersonen dan een impliciete stimulus voor scorekeeping.

Hoewel dit proefschrift dus liet zien dat het scorekeeping mechanisme niet zo alomvertegenwoordigd is als veel evolutionair psychologen beweren, zijn er nog veel vragen onbeantwoord gebleven. Meer onderzoek is nodig naar de precieze "cues", condities en emoties die gerelateerd zijn aan scorekeeping en bonding gedrag. Bovendien is er voor het beantwoorden van de vraag welk mechanisme biologisch primair is, en via wat voor methoden men deze vraag kan beantwoorden, nog veel onderzoek nodig.

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Stellingen bij het proefschrift

'You scratch my back and I scratch yours' versus "Love thy neighbour'. Two proximate mechanisms of reciprocal altruism.

('Voor wat hoort wat' versus 'Heb uw naaste lief'. Twee proximate mechanismen voor wederkerig altruïsme)

Rita Smaniotto

1 Wederkerig altruisme verloopt niet noodzakelijk via een "voor wat hoort wat" (scorekeeping) mechanisme. (dit proefschrift)

2 Het delen van voedsel tussen jagers en verzamelaars wordt over het algemeen beschouwd als een bewijs voor scorekeeping wederkerigheid, maar kan even goed het gevolg zijn van een "heb uw naaste lief" (bonding) mechanisme. (hoofdstuk 2)

3 In tegenstelling tot wat de evolutionaire speltheorie voorspelt, zijn actoren met een relatief onconditioneel coöperatieve strategie in bepaalde omstandigheden beter in staat om een populatie van free-riders binnen te dringen dan actoren met een sterk conditioneel coöperatieve strategie. (hoofdstuk 3)

4 Aan een imbalans in de hoeveelheid gegeven en ontvangen hulp wordt veel minder zwaar getild dan aan een weigering om hulp te geven als men in nood is. (hoofdstuk 4 en 5)

5 Het wel of niet verlenen van een gunst aan een hulpbehoevende bekende die bij de potentiële helper in het krijt staat, is sterk afhankelijk van het soort gunst dat gevraagd wordt. (hoofdstuk 4)

6 De verwachting dat de ander boos zal zijn na een weigering om hem een gunst te verlenen leidt niet tot een toename in de bereidheid tot helpen. (hoofdstuk 5)

7 Gegeven de definitie van sociologie als de wetenschap van de menselijke samenleving en gegeven het feit dat mensen niet de enigen zijn die in groepen leven, is het verbazend dat sociologen zich zo weinig verdiepen in de evolutionaire oorsprong van menselijke (en niet-menselijke) samenlevingen.

8 Gezien de sterke invloed van de aanwezigheid van een *outgroup* op groepsidentiteit, zou een op handen zijnde invasie van de aarde door marsmannetjes wel eens onze beste kans op wereldvrede kunnen zijn.

9 De befaamde *Kretenzer-paradox*, "alle Kretenzers liegen altijd, sprak de Kretenzer Epimenides", is geen paradox.
(Immers, hoewel er een paradox ontstaat als Epimenides' uitspraak waar is, is dat niet het geval als hij niet waar is. Het onwaar zijn van "alle Kretenzers liegen altijd" houdt niet in dat *alle Kretenzers altijd de waarheid spreken*, maar dat *niet alle Kretenzers altijd liegen*.)

10 Getuige de religieuze wortels van de meeste oorlogen, lijken veel predikers van naastenliefde een nogal enge definitie van "naasten" te hanteren.

11 Aangezien de kiezer over het algemeen gericht is op de korte termijn, is het opmerkelijk dat juist de meer "groene" partijen ijveren voor het invoeren van correctief referendum.

12 Tranendal, Koningsoord, Woudbloem, Nooitgedacht, Hongerige Wolf; om het gevoel te hebben in een sprookjeswereld rond te lopen hoef je niet naar Disneyworld maar volstaat een rondje Oost-Groningen.

13 Bezint eer ge bemint.