Building Blocks of Morality:

Reciprocal Altruism and Food Sharing among Chimpanzees (*Pan troglodytes*),

Bonobos (*Pan paniscus*) and other Primates

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To my parents,

with all my love

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Zusammenfassung

Wie von jedem anderen menschlichen Merkmal lässt sich auch von der Moral sagen sie habe eine adaptive Funktion, nämlich den sozialen Zusammenhalt und die Kooperation zu fördern, und damit eine evolutionäre Geschichte. Genauer gesagt wurde vorgeschlagen, dass die menschliche Moral aus sogenannten "Bausteinen" bestehe, d.h. emotionale oder kognitive Mechanismen die auch bei anderen Arten vorhanden sein könnten, insbesondere bei nicht-menschlichen Primaten. Einer der wichtigsten Kontexte in denen solche Bausteine evoluieren können ist der reziproke Altruismus, der Austausch von Gütern oder Dienstleistungen unter Gruppenmitgliedern. Das Hauptziel dieser Studie war daher diese Idee vom reziproken Altruismus als ein Baustein der Moral zu prüfen. Zu diesem Zweck konzentrierte sich dieses Projekt auf den Futterteilenkontext, in dem ein Grossteil der Forschung über reziproken Altruismus sowohl bei menschlichen als auch nicht-menschlichen Primaten durchgeführt wurde. In einer ersten Studie wurden die grundlegenden Bedingungen unter denen Futterteilen bei Primaten evoluieren kann untersucht, mit dem Resultat dass dies der Fall ist wannimmer die grundlegenden Bedingungen für reziproken Altruismus erfüllt sind, was zu erhöhter sozialer Toleranz führt, die sich auch im Futterteilen niederschlägt. Der Hauptteil der empirischen Forschung wurde zum Futterteilen bei Schimpansen und Bonobos, unseren nächsten Verwandten, durchgeführt. Beide Arten teilen im Freiland Futter und dieses Verhalten kann auch in Zoos leicht ausgelöst werden, durch das Zugeben einer monopolisierbaren Ressource. Die Resultate bestätigen, dass eine relativ egalitäre Dominanzhierarchie eine wichtige Voraussetzung für reziproken Austausch ist, da in despotischeren Gruppen das Futter mit Gewalt genommen wird. Ist die Möglichkeit für

reziproken Austausch gegeben, steigt die Motivation zu Teilen und es wird toleranter geteilt. Was die proximate Regulierung angeht, so wird davon ausgegangen, dass Teilen und reziproker Austausch durch selektive soziale Toleranz reguliert werden, und nicht durch berechnende Formen des Austauschs, was hochentwickelte kognitive Fähigkeiten voraussetzen würde. Daher sind die Erwartungen an Futterbesitzer nicht sehr stark und Grosszügigkeit wird nicht belohnt, noch wird Geiz bestraft. Deshalb scheint es keine sozialen Normen zu geben, die dem Futterteilen bei diesen Arten zugrunde läge und die proximaten Mechanismen die es regulieren sind relativ einfach. Schliesslich wurde eine umfassende Literaturübersicht durchgeführt, in der inspiriert von diesen Resultaten untersucht wurde wie bereitwillig eigentlich geteilt oder sonstwie geholfen wird. Aus einer Kombination von Studien zum Futterteilen und künstlicheren Experimenten wurde geschlossen, dass Menschen eine höhere Motivation als andere Menschenaffen zeigen anderen zu helfen. Dies ist im Einklang mit der Naturgeschichte dieser Arten. Schliesslich wurden philosophische Ansichten des Altruismus, bei denen das Erkennen der Bedürfnisse anderer und die Absicht diese zu befriedigen wichtig sind, auf Tiere angewandt. Dies zeigte, dass wohl nur wenige Fälle von biologischem Altruismus auch solchem psychologischen Altruismus entsprechen, denn den Tieren fehlen oft die kognitiven oder motivationalen Voraussetzungen dazu. Zusammen ergeben diese Resultate ein umfassenderes Bild vom System des reziproken Altruismus bei unseren nächsten Verwandten. Trotz beständigen Unterschieden kann man unser eigenes Reziprozitätssystem durchaus als Erweiterung dessen der Menschenaffen sehen, getrieben von den Selektionsdrucken im Laufe der menschlichen Evolution. Auch wenn Futterteilen und andere soziale Interaktionen unter Menschenaffen keine Moral im menschlichen Sinne darstellen, so bilden sie doch die Bausteine aus denen unsere

eigene Moral besteht. Zum Schluss werden einige philosophische Implikationen eines

solchen Verständnisses der Moral diskutiert, insbesondere die Unwahrscheinlichkeit

objektiver ethischer Wahrheiten und die meta-ethischen Positionen die daraus folgen.

Abstract

Morality, like any other human trait, has been proposed to have an adaptive function, namely to promote social cohesion and cooperation, and thus has an evolutionary history. More precisely, it has been suggested that human morality consists of so-called "building blocks", i.e. emotional or cognitive mechanisms that may be shared with other species, in particular non-human primates. One main context in which such building blocks may evolve is reciprocal altruism, the exchange of goods or services among members of a social group. Hence, the main aim of this study was to scrutinize the idea of reciprocal altruism as a building block of morality. To this end, the project focused on the context of food sharing, in which much of the research on reciprocal altruism among both human and non-human primates has been conducted. A first comparative study investigated the basic conditions under which food sharing may evolve among primates, concluding that it does so whenever individuals experience the basic conditions for reciprocal altruism, thus leading to an increased social tolerance, which translates into food sharing. The main empirical research was carried out on food sharing in captive chimpanzees and bonobos, our closest living relatives. Both of these species share food in the wild, and the behavior can easily be induced in captivity by providing monopolizable resources. The results confirmed that a relatively egalitarian dominance hierarchy is an important precondition for reciprocal exchange, because food is taken by force in more despotic groups. Given the possibility for reciprocal exchange, individuals may exhibit higher sharing motivation and share more tolerantly. In terms of the proximate regulation, sharing and reciprocal exchange are thought to be regulated

by selective social tolerance, rather than calculated forms of exchange, requiring advanced cognitive abilities. Hence, the social expectations towards food owners are not very strong and neither is generosity rewarded nor is stinginess punished. Thus, there do not seem to be social norms underlying food sharing among these species and the proximate mechanisms regulating it are relatively simple. Finally, a large amount of review work inspired by these results focused on the question of how voluntarily individuals actually engage in food sharing or other acts of help or assistance. Combining data from food sharing studies and more artificial experimental work, it was concluded that humans show an increased motivation to act on behalf of others relative to the apes, which is consistent with the natural history of the species. Finally, more philosophical views of altruism, including the recognition of another person's needs or desires and the intention to actively satisfy these, were operationalized and applied to non-human animals. It was found that few instances of biological altruism may also represent psychological altruism in a philosophical sense because animals often lack either the cognitive or the motivational preconditions required. These results combine to yield a more complete picture of the reciprocal altruism system of our closest living relatives. Despite consistent differences, our own reciprocal altruism system can be understood as an extension of the apes', expanded by the selective pressures experienced in the course of human evolution. While food sharing and other social interactions among apes thus may not represent morality in a human sense, they do likely constitute building blocks from which our own morality stems. Finally, some philosophical implications of such an understanding of morality as an adaptation with an evolutionary history are discussed, in particular with regard to the unlikelihood of objective truths and the meta-ethical positions that follow from this.

General introduction and conclusions

The core of this dissertation is made up of the five chapters representing original research, including broad comparative analyses using data from the literature (Chapter 1), new empirical work (Chapters 2 & 3), an extensive review of the current literature (Chapter 4) as well as conceptual considerations at the interface of biology and philosophy (Chapter 5). Each chapter was written in a way that makes it stand on its own and has been or will be published individually in scientific journals. Hence, this section aims at placing the work captured in the five chapters in a broader context, introducing their general topics and summarizing their main results, linking the different chapters and drawing some general conclusions. Since this was an interdisciplinary project, the following glossary may be helpful in reading this section (Box 0-1).

Box 0-1*: **Glossary for general introduction and conclusions**

Biological altruism: Behavior that is costly to the actor but beneficial to the recipient

Reciprocal altruism: The exchange of biologically altruistic acts to the mutual benefit of the actors

Psychological altruism: The desire to benefit others as an end in itself, brought about by a change of the actor's preferences upon recognition of the recipients'

Ultimate explanations: Refer to the Darwinian benefits of a behavior, e.g. biological altruism can be beneficial if reciprocated

Proximate explanations: Refer to the motivations of a behavior, e.g. a biologically altruistic act can be brought about by psychological altruism

Prosocial motivation: Any kind of proximate mechanism that can bring about biological altruism

Morality: The rules of conduct in a society, generally functioning to maintain social cohesion and cooperation

Ethics: The philosophy of morality, in particular:

    Normative ethics: Is concerned with whether an act is right or wrong and general principles (ethical theories) underlying such considerations

    Meta-ethics: The philosophy of ethics. Is concerned with the nature of ethical discourse and -theories, moral judgments, etc.

The evolution of "morality"

Ever since Charles Darwin's famous words that "*light will be thrown on the origin of man and his history*" (Darwin 1859 [1985], p. 458), evolutionary biologists have been narrowing the gap between human beings and the rest of the animal kingdom. One by one, traits once believed to be uniquely human were shown to be exhibited too, at least some extent, by other animals. By dissecting apparently complex traits such as culture into simpler components and by identifying the relevant biological mechanisms underlying them, adaptive explanations for hitherto unexplainable traits could be found (e.g. Laland and Galef 2009). But surely, there must be some human characteristics where such a research program fails, finding no trace of homologies or analogies with other animals?

For a long time, morality was believed to be such a characteristic. Even evolutionary biologists such as Thomas Henry Huxley (1989 [1894]) were convinced that evolution by natural selection could not explain why humans should strive to be good and respected members of society, concluding that our culture had somehow allowed us to conquer our otherwise selfish nature. Others followed similar arguments, including Richard Dawkins (1976), who concluded that only we humans had managed to overcome the tyranny of our selfish genes. However, other researchers were soon to show that selfish genes do not necessarily produce selfish agents.

In two landmark papers, William Hamilton (1964) and Robert Trivers (1971) introduced the mechanisms of kin selection and reciprocal altruism to explain how genes coding for altruistic behavior may thrive in a population. The general principle is the same in both mechanisms: altruistic behavior has to be discriminately directed towards those who are likely to carry the same altruistic alleles, either because they are

close relatives, or because they have exhibited past behavior that is indicative of these altruistic alleles.

While fundamentally based on the logic of natural selection and population genetics, both processes also make predictions about the proximate mechanisms of behavior. In particular, Trivers (1971) has elaborated greatly on the psychological regulation required to achieve the maximum return-benefits from reciprocal altruism among humans, including the building of friendships with other altruists, the feelings of sympathy to elicit help and gratitude to ensure reciprocation as well as their fine-tuning to the cost/benefit ratio of the act, the feeling of indignation when cheated upon and the use of "moralistic aggression" to counter and educate cheaters and finally the resulting feeling of guilt, reparative altruism and conscience in order to prevent or mitigate the costs of moralistic aggression. Thus, it can be seen that many of the sentiments and cognitive processes relevant for morality may in fact have their origin in such a simple biological mechanism as the reciprocation of acts of help or assistance.

Building on these ideas, Wilson (1975) in his book *Sociobiology* was soon to claim that the study of morality (and other topics) had to be taken away from the social scientists and philosophers. The latter's response is outlined below, in the section on evolution and ethics. However, the first relevant question is, how do biologists actually *define* morality? Due to the sociobiologists' inherent interest in natural selection and the cost/benefit ratios of behavior, a nearly exclusive focus on the ultimate level of explanation prevailed in the early discussion of morality. Indeed, many sociobiologists seemed to equate morality with (biological) altruism, taking for granted the sophisticated psychological mechanisms that may result from it, and that are usually the main interest of social scientists and philosophers. Some definitions expanded the

framework of reciprocal altruism, requiring that interactions go beyond the dyadic level and that third parties participate in the game of exchanging altruistic acts, accusations, punishment, etc. thus leading to group-level norms (Alexander 1987; DeScioli and Kurzban 2009). Here I will tentatively subscribe to such a functional definition of morality as a multiplayer game (Figure 0-1), in which group-wide norms make individuals incur short-term costs in order to maximize everyone's long-term benefit. However, it is crucial that the proximate mechanisms necessary to uphold such a system are also well described and understood, as a contribution of biology to moral philosophy is otherwise very limited.

One important step in understanding this proximate regulation and the selective pressures that produce it was to take a comparative approach. In particular, the study of our closest living relatives, the primates, has contributed greatly to this, as described in the next section.

Third Party
(praise, condemnation)

reward, punish

cooperate, cheat

reciprocate, punish

Actor
(sympathy, conscience)

Second Party
(gratitude, indignation)
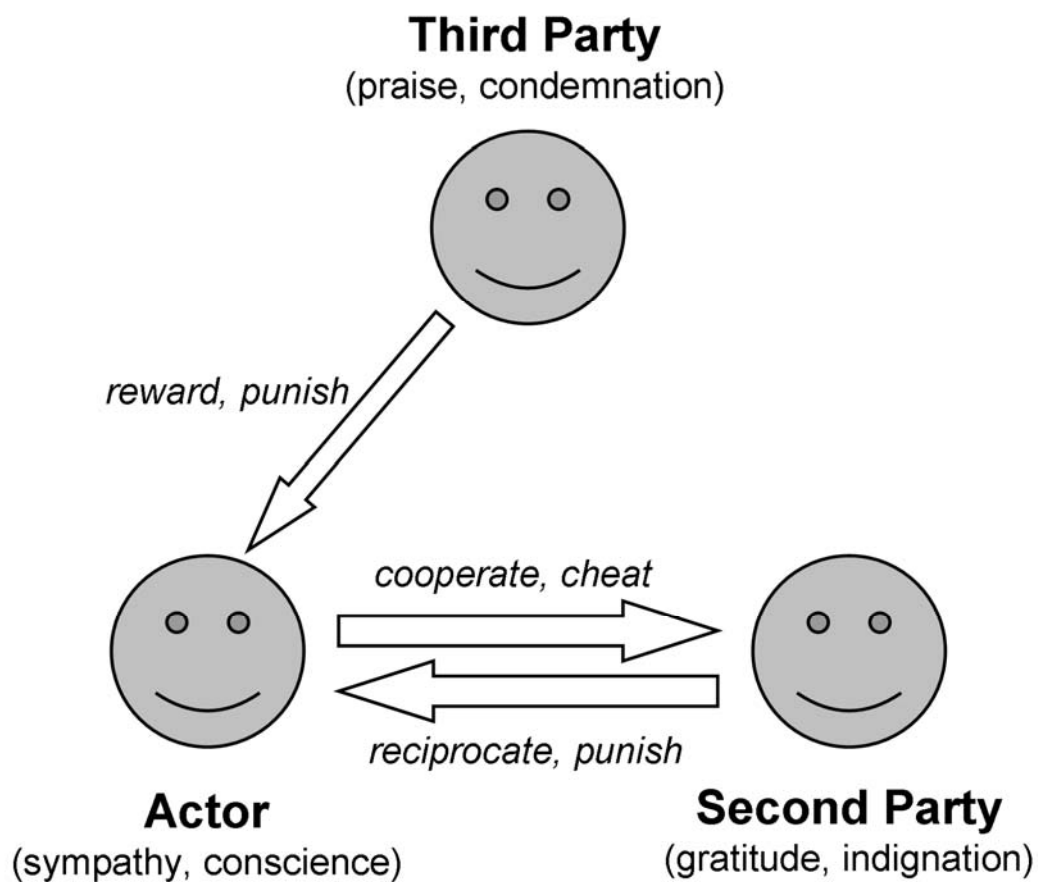
Figure 0-1: The dynamics of morality as a (at least) three-player game. Indicated along the arrows are the actions the players may take and in brackets are the proximate mechanisms that produce them. In a positive sense, actors may help others out of feelings of sympathy, thus receiving both gratitude and praise by second and third parties respectively, leading to the benefits of direct or indirect reciprocity. In a negative sense, actors develop a conscience in order to counter not only indignation by second parties but also condemnation by third parties, as a protection against punishment. These dynamics can lead to the establishment and maintenance of group-wide norms

Building blocks of morality

As Darwin already noted in his book on the descent of man, evolution of morality by natural selection is not necessarily restricted to mankind. Indeed, „*Any*

animal whatever, endowed with well-marked social instincts ... would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well, or nearly as well developed, as in man" (Darwin 1982 [1871], pp. 71-72). Hence, a moral sense or conscience could potentially be found in other animals as well. This idea has been pursued most seriously and persistently by Frans de Waal who eloquently argued in several books and papers that human morality is made up of "building blocks" already present to some extent in other animals, in particular non-human primates (de Waal 1996; Flack and de Waal 2000; de Waal 2006; see Figure 0-2). Over the past decades, he and others have gathered a large amount of evidence for such building blocks (ibid.). While other researchers tend to emphasize human uniqueness (e.g. Fehr and Gachter 2002; Fehr and Fischbacher 2003; Gintis et al. 2008), de Waal argues that there are no discontinuities between humans and non-human primates in terms of morality. In his view, the only uniqueness of human morality is that it combines all the building blocks already present in some or other primate species (Figure 0-2). However, in emphasizing continuity, de Waal's account lacks a clear definition of human morality and a proper discussion of how and why humans differ from their relatives in the extent of their morality (Kitcher 2006a).

Hence, the main aim of this thesis was to scrutinize this idea of a continuum between "building blocks" of morality among primates and human morality, in particular with regard to reciprocity and altruism. To this end, these proposed building blocks were studied among our closest living relative, chimpanzees and bonobos. Comparisons with other species including humans in exhaustive review work as well as some philosophical considerations complete the study. The main results are summarized in the next section.
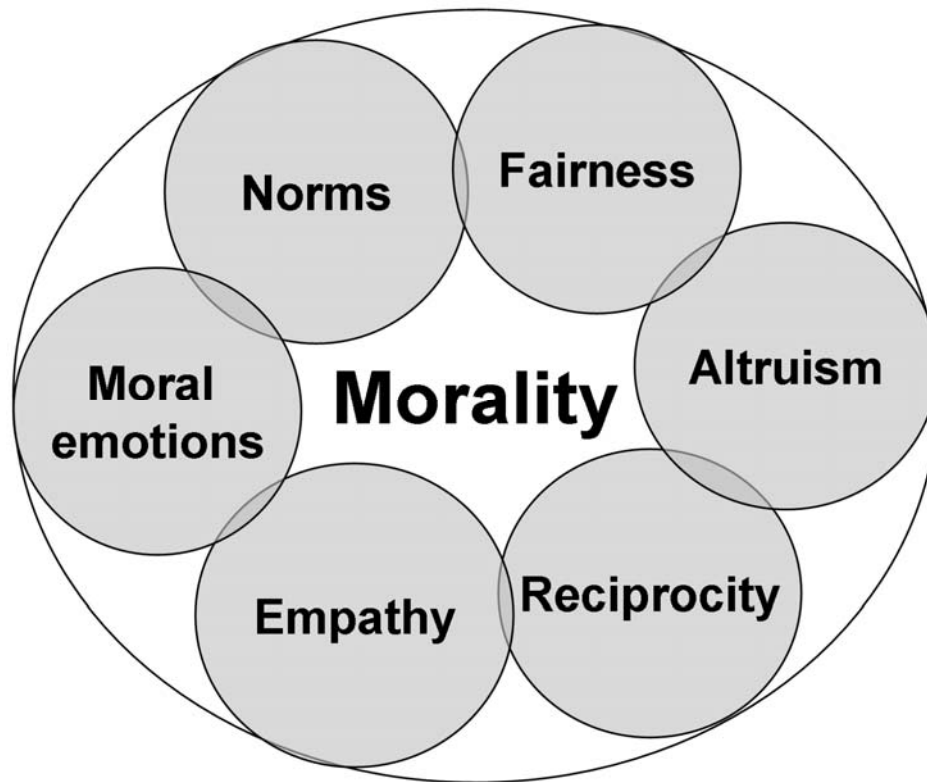
Figure 0-2: Morality as seen by de Waal (1996, 2006) consists of several "building blocks", for which he has gathered a large amount of evidence in different primate species. In his view, the only difference between humans and other primates is that in humans all these building blocks are present, thus representing full morality. Figure adapted from a lecture by de Waal at the University of Zurich in 2008

Reciprocal altruism and food sharing: main results of this study

Much of the empirical research concerned with the evolution of moral building blocks has focused on some form of reciprocity (Trivers 1971; Alexander 1987) and food sharing has been a main context in which reciprocity under natural conditions has been studied both among human and non-human primates (Feistner and McGrew 1989; de Waal 1996; Brown et al. 2004; Gurven 2004; de Waal 2006). Hence, this project

focused mainly on this context and tried to answer a variety of questions both on the ultimate and the proximate level of explanation.

In particular, Chapter 1 deals with the very basic question of why food sharing evolved in some primate taxa but not others. Using data from the literature, we applied comparative evolutionary analyses to test different underlying factors. We could show that food sharing evolved if the very basic conditions for reciprocal altruism were fulfilled (Box 0-2) and individuals thus experienced some need of negotiating the exchange of various services. Hence, we argue that species that encountered these conditions evolved higher levels of social tolerance that are then expressed in food sharing.

Box 0-2: The basic conditions for reciprocal altruism (after Trivers 1971)

- *A* can provide a service/resource to *B*, the costs of which are smaller than the benefits to *B*
- *B* cannot acquire the service/resource by force
- On other occasions, *B* can provide the same or another service/resource to *A*

In Chapter 2, we further examine the basic conditions for reciprocal altruism by comparing reciprocity in food sharing and grooming across different groups of chimpanzees and bonobos. We found that reciprocity declined with increasing steepness of the hierarchy as dominants in more despotic groups could acquire resources by force, thus precluding reciprocal exchange (Box 0-2). Conversely, we found that in those groups in which reciprocity was more likely, food was also shared more tolerantly, thus leading over to more proximate mechanisms of reciprocal altruism.

Using the same data for Chapter 3, we tested whether reciprocal exchange was contingent on previous interactions, thus indicating calculated reciprocity, and whether individuals that did not share food received punishment by others. We found no evidence for the latter and although there was some evidence for contingent exchanges as bonobos allowed more food transfers after having been groomed, we prefer a parsimonious emotional explanation over a highly cognitive one. Thus, we conclude that reciprocal exchange among chimpanzees and bonobos is mediated by tolerance, which may temporarily be increased through grooming, rather than by calculated exchange. We suggest that this grooming effect may explain most instances of contingent reciprocity among primates and that although not beyond the cognitive capacities of primates, calculated exchanges only became important recently in human evolution as the basis of trade between relatively unfamiliar individuals.

In Chapter 4 we asked the more general question of how readily humans and other primates engage in acts of help or assistance, what external factors make them do so and how psychological differences between species can be explained by their natural histories. Using a large amount of data from the literature, we quantified food sharing among primates into proactive, reactive and passive transfers, each representing a different psychological regulation. We found that the vast majority of food transfers were passive, thus indicating low prosocial motivation, some were reactive, indicating a response to the recipient's need and only some primate taxa regularly engage in proactive sharing, indicating a high prosocial motivation. Together with an exhaustive review of recent experimental work, we use these data to argue that humans have acquired a different prosocial psychology relative to other apes, probably due to the adoption of cooperative breeding and indirect reciprocity.

Finally, in Chapter 5 we note differences between biological and philosophical views of altruism and discuss difficulties in testing the latter ones. We examine the cognitive and motivational preconditions for psychological altruism and discuss whether animals could have it and how we could recognize it. We propose that if *A* is an intentional agent, as indicated by a well-developed theory of mind, and *A* changes its behavior, thus indicating a change in intentions, in order to satisfy *B*'s intentions, as perceived by *A*, and if other immediate reasons for this change in behavior such as harassment can be excluded, then *A*'s behavior is indicative of psychological altruism. Referring mainly to Chapter 4, we propose that only few instances of biological altruism may also represent psychological altruism, because species lack either the cognitive- and/or the motivational preconditions, and discuss whether and why humans differ in their expression of psychological altruism.

Some of these results are summarized in Figure 0-3. Basic conditions for reciprocal altruism can explain why food sharing should occur at all, whereas the average certainty of return benefits can explain the level of sharing motivation that has evolved in a particular species. Combined with advanced cognitive skills, high sharing motivation may reflect psychological altruism. Thus, we conclude that building on the cognitive and psychological predispositions already present in the last common ancestor with chimpanzees and bonobos, humans have substantially extended these building blocks of morality. This was probably due to an ever increasing interdependence and the resulting need for social cohesion and cooperation, from the loose communities of great apes to cooperatively breeding hunter-gatherer bands and modern global societies. Thus, human morality is characterized by a strong desire to adhere to social expectations and

norms and reward those that do likewise. On the negative side the conscience prevents

transgression of norms lest one evoke indignation and punishment (cf. Figure 0-1).
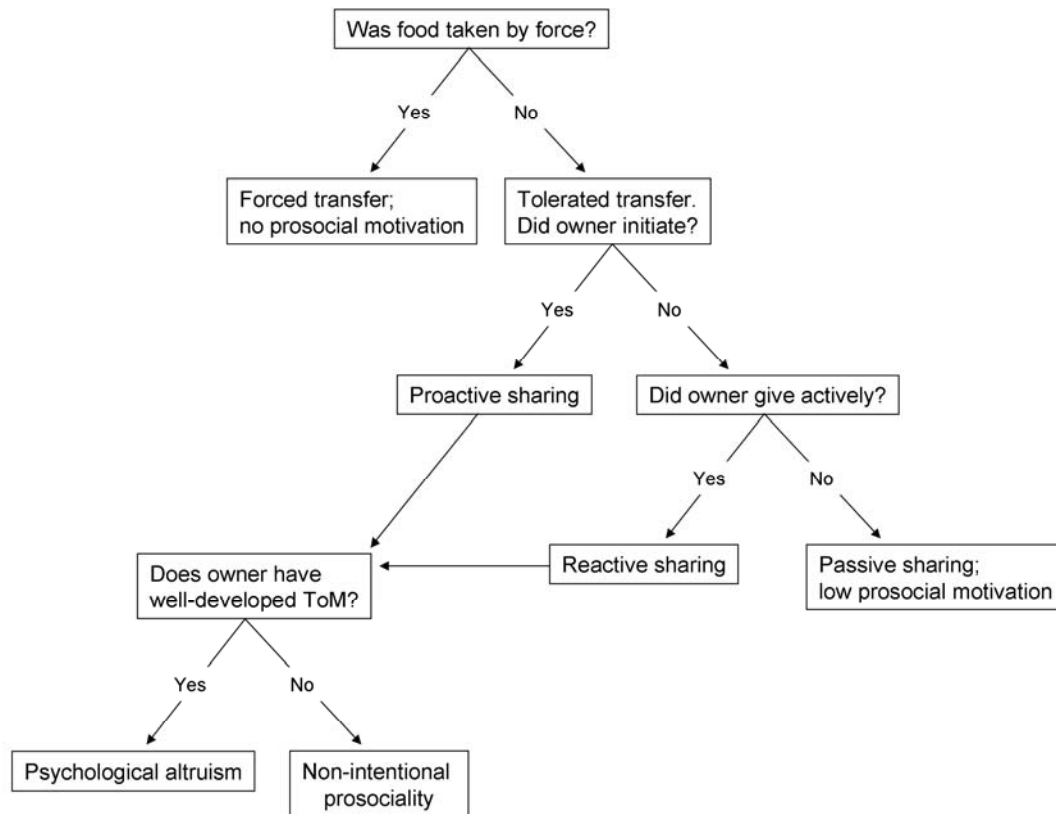
Figure 0-3: A flow diagram summarizing all possible ways in which food could be transferred from

owner to recipient. In despotic species, dominants can take food by force, no reciprocal exchange

should occur and consequently owners should have no motivation to share (Chapters 1 & 2). In

egalitarian species, owners should have some prosocial motivations and tolerate transfers if the

roles are frequently reversed or if there are other resources or commodities to be traded (Chapters

1 & 2). Calculated exchanges however are not common in primates (Chapter 3). Proactive sharing

reflects a high intrinsic prosocial motivation and is only regularly found among cooperative

breeders (Chapter 4). Reactive sharing reflects a response to the recipient's need and occurs

occasionally among apes, in particular chimpanzee males (Chapter 4). Passive sharing indicates a

lack of intention and thus reflects low prosocial motivation (Chapters 4 & 5). If owners share

proactively or reactively and have a well-developed theory of mind (ToM), thus suggesting a change

in intentions due to recognition of the recipients' intentions, then psychological altruism may be

inferred (Chapter 5).

Chimpanzees and bonobos as study species

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are our closest living relatives and many studies have shown amazing similarities between them and us in terms of social behavior, cognition, emotions, etc. (de Waal 1996; de Waal 2006), thus making them ideal and invaluable study species for understanding human evolution (Figure 0-4). Together they form our sister taxon as they split from their most recent common ancestor roughly 1.5-2 million years ago through the formation of the Congo river and are thus equally closely related to humans (Stumpf 2007). However, chimpanzees have been far better studied, both in the wild and in captivity (Stanford 1998; Stumpf 2007). This is largely due to the fact that bonobos are relatively rare in captivity and have been difficult to study in the wild because of political instabilities in the only country they occur, the Democratic Republic of Congo (ibid.). As a consequence, early studies had a large impact on the public perception of bonobos (Stanford 1998), leading to the popular image of the "hippie primates" that make love and not war, in contrast to chimpanzees who are thought of as more violent and brutal (de Waal 2005). More recent research has proven such a dichotomous view wrong, showing that levels of aggression and affiliation are clearly affected by experienced levels of competition and thus probably lie on a continuum spanning both *Pan* species (Stumpf 2007; Stevens et al. 2008). Thus, although undoubtedly some differences exist in terms of socio-sexual behavior, female dominance and possibly cognitive development (Stumpf 2007; Wobber et al. 2010), the two species are treated as largely equal for the purpose of this thesis and differences found between them are explained in terms of general social factors rather than as species idiosyncrasies.

Figure 0-4: Chimpanzees (left) and bonobos (right) during the course of a food sharing experiment. The chimpanzees were observed at the Abenteuerland Walter Zoo in Gossau SG (Switzerland), the bonobos at the Dierenpark Planckendael (Belgium). The chimpanzee picture shows the alpha male, Digit, sharing with a young female, Elisha. The bonobo picture shows the young male Zamba and his mother Hortense investigating the bag with food as another female, Djanoa, watches and the alpha female, Hermien, approaches in the background

Evolution and ethics

An important question arising from a biological study of morality is whether such a research program can make any contributions to moral philosophy, in particular normative ethics or meta-ethics. Wilson's (1975) and other sociobiologists' proposals of naturalizing morality (let alone earlier attempts by social Darwinists) were initially met with little enthusiasm on the part of moral philosophers (Kitcher 1985; Ruse 1986; Kitcher 2005). Many philosophers rejected the very idea based on the objection of the naturalistic fallacy, i.e. that an *is* can never lead to an *ought* (Hume 2003 [1739-1740]). Thus, the biological sciences have to contain themselves with describing the world as it is, while only moral philosophy may deal with questions of how the world ought to be. Other common objections include that (i) altruism neither fully represents nor describes

morality, (ii) that morality cannot be functionalized in terms of costs and benefits, or (iii) that a knowledge of ultimate factors (costs and benefits) cannot advance moral discourse, -judgment, -reasoning, etc. (e.g. Peacock et al. 2005).

More recently, an increased focus on proximate mechanisms drawing mainly from advances in primatology (de Waal 1996; de Waal 2006) and neuroscience (Haidt 2001) has led to the general acceptance of the idea that human beings' capacity for sympathy, which is at the basis of important schools of moral philosophy (Smith 2002 [1759]; Hume 2003 [1739-1740]), may have evolved through natural selection (Sober and Wilson 1998; Kitcher 2006b). Furthermore, the novel fields of experimental philosophy and moral psychology have started to investigate empirically how humans respond to moral dilemmas, how they make moral judgments, etc. (Nichols 2004; Hauser 2006; Haidt 2007). Thus, the naturalization of morality is now well on its way. However, it is still not clear whether naturalizing morality has any implications for moral philosophy.

Two philosophers in particular, Michael Ruse and Philip Kitcher, have taken the idea of morality as an adaptation with an evolutionary history seriously and have led the investigation of its philosophical implications (Ruse 1986; Kitcher 1998; Kitcher 2003; Kitcher 2006b; Ruse 2009). Both seem to agree on the fact that morality represents a kind of social contract that was not made by conscious agreement but set in place by our genes through natural selection. However, they do differ in their main conclusions.

Ruse states somewhat provocatively that "*ethics is an illusion put in place by natural selection to make us good cooperators*" (2009, p. 297) and goes on to make the meta-ethical inference that there are no objective moral justifications, hence one is inevitably driven to skepticism about the foundations of ethics. Thus, the Darwinian

approach to ethics in Ruse's view leads to a kind of "moral non-realism" (Ruse 1986).

In this view, right is right and wrong is wrong just because that is the way we feel about

it, there is no higher appeal. He adds that the fact that we feel not only compelled to do

right and accuse wrong, but are also convinced that there are objective foundations for

doing so, is itself a biological adaptation, because otherwise morality would collapse

into futility: "*morality stays in place as an effective illusion because we think that it is

not an illusion but the real thing*" (Ruse 2009, p. 310). He concludes by reassuring the

reader that our belief in this illusion is so strong that seeing through it does not lead to

its abandonment.

Kitcher takes a slightly more cautious approach. He starts from the observation

that "*the ethical practices of contemporary human groups have a long history, one that involves

the emergence under natural selection of various emotions and psychological capacities, as

well as a sociocultural evolution.*" (Kitcher 2006, p. 13). Understanding current ethical practices

as a product of such a history then casts doubt on claims of there being one (or several)

fundamentally true basic ethical principle(s), an idea inherent to most contemporary ethical

theories. However, there remains, in Kitcher's view, a sense of ethical progress throughout this

history that is independent of such moral truth. Rather than by increasing moral truth, ethical

progress occurs through fostering social cohesion and cooperation, which is the primary

function of morality. In particular, this is achieved by the expansion of capacities for

psychological altruism, including for example an ever growing circle of potential recipients.

Kitcher concludes by suggesting that "*armed with an account of ethical progress, the

naturalistic ethics I envisage could take up the project of normative ethics in a distinctive way.*"

(Kitcher 2006, p. 28), namely by replacing the "blind lurchings of history" with a more

methodological quest for ethical progress. However, he remains rather vague about how such a

quest should be organized.

In summary, taking a biological account of morality seriously can lead to highly interesting philosophical conclusions. Thus, an original aim of this thesis was to further explore the possible implications of biological views of morality on moral philosophy and in particular meta-ethics. However, given the complexity and diversity of the field and the difficulty of such an approach (Kitcher 2005), this ambitious project had to be abandoned for now. Instead, I could merely begin to understand the current debates in meta-ethics, with positions like Ruse's and Kitcher's and their critics, and let some of the work in this thesis be inspired by philosophical viewpoints (Chapter 5). Future work will have to advance the debate on naturalistic ethics.

Conclusions: Continuity or discontinuity?

In almost all of the chapters, we have found some differences between humans and non-human primates. However, this is not necessarily to say that the human species is unique in any sense other than in the way every species is unique through its own evolutionary history. Rather, the fact that almost all unique human traits related to morality, or at least related to reciprocity and altruism as treated in this thesis, have some homologies or analogies in other species, and that the acquisition of derived human traits can be explained through processes of natural selection, places humans firmly amidst other animals. For instance, the fact that only humans may have a full-blown belief-desire psychology and second order intentionality need not preclude the possibility that other animals can be psychological altruists (cf. Chapter 5). Indeed, it merely serves to challenge any definition of psychological altruism based on such narrow cognitive preconditions. Thus, I support the notion that human morality can be

understood as consisting of "building blocks", i.e. emotional and cognitive processes with a specific function that have an evolutionary history and are partly shared with other species (de Waal 1996; de Waal 2006).

Having said this, I think that there are some important aspects of human morality that are probably not shared with other animals (but that are nonetheless understandable as an extension of animal precursors). As mentioned above, I tentatively subscribe to a (functional) definition of morality that goes beyond the dyadic level of interaction (Alexander 1987; DeScioli and Kurzban 2009; Figure 0-1). Importantly, multiplayer dynamics bring some changes in the proximate regulation of the reciprocity system, which are, I think, relevant to morality. For instance, while conscience may already develop in direct reciprocity systems, if there is punishment, the fact that a cheater may face condemnation *by any individual* of its community should certainly have made it stronger. Hence the extreme sensitivity of humans to cues of being watched and the feeling of guilt even in private (cf. Chapter 4), leading to a strong adherence to social norms. Conversely, expectations about others' behavior, that were only based on an individual's own past interactions in direct reciprocity systems, now become adjusted to those of others, thus leading to *shared expectations* and eventually group-wide norms. There is as yet no strong evidence that would suggest that chimpanzees (or other species) engage in such group-level dynamics (but see Rudolf von Rohr et al. in prep.). Thus, my tentative conclusion is that a full morality in the sense we know it requires such group-wide norms, and that its evolution can be understood by the multiplayer dynamics of fission-fusion foraging societies with high interdependence which led to the adoption of ever stronger expectations, rules of conduct, conscience, etc. (Alexander 1987).

Finally, in terms of philosophical implications of a naturalized view of morality, I agree with both Ruse and Kitcher that there is little room for objective moral truth. I am sympathetic to a Kitcherian kind of position that recognizes the general principles leading to the (biological and cultural) evolution of our current ethical practices and attempts to *actively apply* these in order to advance ethical progress in the sense of promoting social cohesion through an expansion of our capacities for psychological altruism. I am aware that this position is not invulnerable to the problems of naturalistic fallacy, since it turns a fact (ethical progress) into a purpose. However, seeing that abandoning it would leave no other option than to adopt a Rusean moral skepticism, and that we are clearly still in need of promoting social cohesion and cooperation in a global society, I do not think that many people would question this purpose.

Chapter 1: The evolution of food sharing among primates: Valuable relationships and reciprocal exchange

Food sharing refers to the un-resisted transfer of food from one individual to another, thus reflecting high social tolerance. While sharing with infants is explained by nutritional or informational benefits to the offspring, sharing among adults is often explained by reciprocal exchange, such as food-for-sex or food-for-support. We group various hypotheses invoking reciprocity under the valuable-relationships hypothesis, which states that the necessity of exchanging social services led individuals to evolve strong bonds with high social tolerance, sometimes expressed in food sharing. We tested these hypotheses in a sample of 68 primate species with phylogenetic analyses using both maximum likelihood and Bayesian approaches. We found only weak support for the informational hypothesis for sharing with infants and no support for the nutritional hypothesis. However, sharing with infants emerged as a necessary precondition for the evolutionary emergence of food sharing among adults. The evolution of sharing among adults, in turn, was strongly correlated with the presence of valuable relationships. In particular, sharing from males to females was explained by the opportunity for female mate choice ("food-for-sex") and sharing among males and among females by the presence of male-male and female-female coalitions respectively ("food-for-support"). Thus the valuable relationships hypothesis was strongly supported. We discuss possible constraints on the evolution of sharing, such as despotism and attractiveness of the diet, and make predictions about other species not included in the sample. We conclude by drawing inferences to the evolution of sharing in humans.

Introduction

Food sharing (henceforth: "sharing") is universal among human foragers, and an expression of high social tolerance. This phenomenon is probably adaptive due to the combined benefits of kin selection, reciprocity and costly signaling (Gurven 2004). However, interactions over food among most animals are generally hostile, with stronger, more dominant individuals taking food from others by force. Such behavior is often termed *klepto-parasitism* (Hamilton 2002; Morand-Ferron et al. 2007) and explained by direct benefits to the dominant individual and the high costs of defending food for the subordinate. In some taxa however, sharing serves important social functions, mainly in the context of mating, such as in courtship feeding among birds (Lorenz 1965) or nuptial gifts in insects (Vahed 1998). Similarly, among many primate species sharing is thought to serve social functions and is relatively wide-spread, both from adults to infants and among adults (Feistner and McGrew 1989; Brown et al. 2004). The aim of this paper is to trace the evolution of sharing among primates, by identifying necessary preconditions and functional benefits for this behavior.

Following Feistner and McGrew (1989) we define sharing as un-resisted transfers from one individual holding food (owner) to another (beggar). Almost inevitably, this is an altruistic act, since the owner incurs a cost and the beggar gains a benefit. Similar to other altruistic acts such as grooming or agonistic support, most hypotheses explaining sharing among primates thus invoke either kin selection or some form of reciprocity as ultimate mechanisms. Proximately, relatives or non-relatives in species relying on such mechanisms form strong bonds or friendships characterized by high tolerance, one expression of which is the exchange of various altruistic acts (Silk 2002; Silk 2006) and sharing is expected to follow the same pattern. Since food

ownership is often biased towards dominants, reciprocal exchange is thus expected

when subordinates have leverage over dominants because of their value as social

partners (Lewis 2002). Below we summarize the relevant hypotheses proposed for

sharing among primates and derive predictions to be used in comparative analyses,

based on scores of sharing in a large sample of species.

As for courtship feeding among birds, which is highly correlated with the

provisioning of juveniles (Moller and Cuervo 2000) and employs the same behavioral

patterns (Lorenz 1965), it is likely that sharing among primates first emerged in the

context of sharing with infants, before it could be recruited to serve social functions

among adults. Hence, in order to trace the evolution of sharing among primates in

general, we first have to explain why adults share with infants. We then have to

establish whether the presence of this behavior could be a precondition for sharing

among adults, or, in other words, whether sharing among adults was derived from

sharing with infants (Tinbergen 1952). Finally, we go on to test adaptive hypotheses for

sharing among adults. Identifying the general factors responsible for sharing in primates

will help elucidate the evolution of this behavior in humans.

Hypotheses and predictions

<u>Sharing with infants</u>

- *Nutritional hypothesis*: This hypothesis presumes that sharing provides infants
  with valuable extra nutrients, thus increasing growth rates and facilitating
  weaning (Brown et al. 2004). Hence infants should preferably beg for high
  quality food, which leads to the prediction that the *quality of the diet* favors
  sharing with infants.

- *Informational hypothesis*: Sharing provides infants with valuable information about the affordances of food items that are too difficult for them to process independently (Brown et al. 2004). Hence infants should beg for difficult-to-process items, leading to the prediction that the *difficulty of the diet* favors sharing with infants.

Sharing among adults (any dyad)

- *Derived-behavior hypothesis*: We propose that similar to courtship-feeding among birds, sharing among adults is derived from *sharing with infants*. Hence, we predict that the presence of the latter trait influences the presence of the former.

- *Sharing-under-pressure (also: tolerated theft, harassment)*: Beggars are so persistent that the costs of defending food exceed the costs of relinquishing parts of it, hence owners allow beggars to take some food in order to be left alone to consume the remaining food (Blurton Jones 1984; Stevens and Stephens 2002).

Note that while these two hypotheses explain why sharing among adults should occur *at all*, they make no prediction for the *direction* of transfers. In particular, several authors noted that the sharing-under-pressure hypothesis is not mutually exclusive with other hypotheses (Stevens and Gilby 2004; Gilby 2006; Jaeggi et al. 2010b), which makes it difficult to test in a comparative analysis. Here we assume that most sharing among primates is essentially "under pressure", since food transfers are predominantly passive (Brown et al. 2004; Jaeggi et al. in press). In contrast, the following hypotheses explain why *particular* owner-recipient dyads should share.

Sharing among adults (particular dyads)

 In general, all the following hypotheses invoke reciprocal exchange, or in proximate terms, high tolerance towards valuable relationship partners. Food is shared with specific partners (or more precisely: specific partners are allowed to take food) because this increases the probability that the partner will provide rather than withhold a valuable service in the future (e.g. agonistic support or mating), resulting in reciprocal exchange patterns. The necessity to allow others to take can thus be explained in terms of subordinate leverage (Lewis 2002). Depending on balance or bias of ownership, sharing will then be traded for itself or for other services. In most cases, ownership is biased towards dominants within sexes and towards males between the sexes, and sharing is thus often traded for other currencies. Proximately, food is shared with specific partners because reciprocating individuals form strong social bonds, one expression of which is the tolerant sharing of food. Thus, all the following hypotheses may be grouped under the header *valuable-relationships hypothesis*.

- *Mate choice (food-for-sex)*: Commonly known as the meat-for-sex hypothesis, it is often assumed that males "buy" immediate mating benefits with high value food. However, in the simplest form, females may take ubiquitous food in order to test a male's tolerance, ending association with the male if he does not comply (van Noordwijk and van Schaik 2009). Even among the better known examples of chimpanzees or bonobos, sharing is predominantly passive, direct exchanges of food and matings (in the short term) are rare and males also commonly share with lactating females (reviewed by Gilby et al. in press). Hence sharing is better seen as an expression of long-term tolerance that might eventually relate to higher mating success. Thus the hypothesis can be formulated more generally: Whenever females can exert mate choice, males

should allow females to take food in order to increase their chances of mating with the female in the future (Gomes and Boesch 2009; van Noordwijk and van Schaik 2009). In more proximate terms, it could be said that in the presence of female choice, males and females may form social bonds, one expression of which is the sharing of food. Hence we predict that the *opportunity for female choice* favors sharing from males to females.

- *Coalition partners (food-for-support)*: Similar to the mate choice hypothesis, it can be said that food is "traded" for support. However, evidence for short-term exchange in this context is also largely lacking and sharing is better seen as an expression of long-term bonds among allies (Nishida et al. 1992; Watts and Mitani 2002; Mitani 2006). Hence this hypothesis can also be formulated more generally: Whenever individuals depend on support from others who can provide or withhold such support, owners should allow recipients to take food in order to increase the chances of support being provided in the future. Or, in more proximate terms, individuals should develop social bonds with potential allies, one expression of which is the sharing of food. This should hold true for both males and females. Hence we predict that the presence of *coalitions* favors sharing within the sexes. (Of course, among female primates, coalition partners are often matrilineal kin. But, not all females necessarily develop strong bonds with their kin (e.g. orangutans, who do not form coalitions), and others form bonds with non-kin (e.g. bonobos, who do form coalitions). Hence the prediction holds for kin and non-kin alike. In the end, the evolution of coalitions and food sharing among female primates) can be linked to the presence of contest competition.)

- *Pair-bonds*: Monogamous pairs develop strong bonds due to the shared demands of child care and protection from infanticide (Palombit 1999). These pair-bonds usually foster high tolerance among the mates, sometimes expressed in sharing (e.g. Fragaszy and Mason 1983; Wright 1984). In particular, lactating or pregnant females, with high nutritional demands, are often allowed to take food from their partners (e.g. Wolovich et al. 2008a; Wolovich et al. 2008b). This leads to the prediction that *monogamy* favors sharing from males to females.

- *Polyandry/Polygyny*: A few studies also noted transfers among males or females of facultatively polyandrous (Saguinus fuscicollis: Goldizen 1989; Pithecia pithecia: Homburg 1997) or polygynous groups (Nomascus concolor: Fan and Jiang 2009) respectively. Presumably, the partners in these groups were siblings, supporting each other's reproductive effort, which could explain the high tolerance displayed in sharing. Unfortunately these social organizations are too rare for this hypothesis to be tested with a comparative analysis.

Methods

Comparative data

We reviewed the literature on sharing in primates and compiled an exhaustive up-to-date list of 168 references related to sharing (Table 1-1). Species were included in the analysis if either sharing had been reported or if no sharing had been reported despite considerable study effort (at least 10 behavioral studies on the species listed in ISI Web of Knowledge by end of 2009). Sharing with infants was quantified as either absent (0), present (1: mentioned occasionally) or common (2: more than one study

explicitly addressing sharing). Sharing among adults was quantified as present or absent and we specifically scored sharing between particular dyads, namely from males to females, among males and among females. Sharing from females to males was too rare to test. Thus, a total of 68 primate species could be included in the comparative sample (Table 1-1).

Predictor variables

The predictions derived from the hypotheses listed in the introduction were operationalized as follows:

- *Quality of diet*: Continuous variable, based on the diet quality index as defined by Fish & Lockwood (2003):

$$DQ = 0.33L + 0.67F + M$$

where DQ is the index of diet quality, and L, F, and M are the percentages of time spent foraging for leaves and other vegetative plant parts, fruit (including gum and flowers), and meat (indeed, any animal matter), respectively. The possible range of DQ values is 0.33–1. The values were obtained directly from Fish & Lockwood (2003) or calculated from Rowe (1996). If numbers were unavailable for a species, the value of the sister species was used.

Difficulty of diet: Ordinal variable, based on Gibson's (1986) classification of non-extractive foragers (0), un-skilled/specialized extractive foragers (1) and skilled extractive foragers (2). In contrast to Gibson we classified *Pongo* as skilled extractive foragers since there is now good evidence for complex extractive foraging skills such as tool-use (van Schaik et al. 1996) and that skills

are acquired through prolonged periods of social and individual learning in both

orangutan species (Forss 2009; Jaeggi et al. 2010a).

-   *Opportunity for female choice*: binary variable, are multiple males commonly

    present during foraging? If different types of foraging groups commonly occur

    in a species, e.g. monogamous pairs and multi-male single-female groups, the

    multi-male score is given. Source: Rowe (1996)

-   *Coalitions*: binary variable, do same-sex coalitions occur in this species? Source:

    Plavcan et al. (1995)

-   *Monogamy*: binary variable, is the species socially monogamous? If different

    types of social organization occur, the monogamy score is given. Source: Rowe

    (1996)

Table 1-1: List of all the species included in the comparative analyses and the variables of interest

Species[a]	FS inf.	FS ♂-♂	FS ♀-♀	FS ♂-♀	Diet diff.	DQI	♂-♂ coalitions	♀-♀ coalitions	Monog.	♀ choice	Ref.[b]
Alouatta palliata	1	0	0	0	0	0.43	0	0	0	1	1-4
Aotus azarae	2	0	0	1	0	0.65	0	0	1	0	5-7
Ateles geoffreyoi	1	0	0	0	0	0.61	1	0	0	1	8-10
Callicebus moloch	1	0	0	1	0	0.59	0	0	1	0	11,12
Callicebus torquatus	1	0	0	0	0	0.65	0	0	1	0	13
Callimico goeldii	2	0	0	0	0	0.67	0	0	1	0	14-17
Callithrix argentata	2	0	0	0	1	0.67	0	0	1	1	18-20
Callithrix jacchus	2	0	0	1	1	0.67	0	0	1	1	21-32
Callithrix pygmaea	2	0	0	0	0	0.67	0	0	1	0	33,34
Cebus albifrons	1	1	0	1	1	0.67	1	0	0	1	35
Cebus apella	1	1	1	1	2	0.87	1	1	0	1	36-43
Cebus capucinus	1	1	0	1	2	0.65	1	0	0	1	44-46
Cebus olivaceus	0	0	0	0	2	0.87	0	0	0	1	
Cercocebus atys	0	0	0	0	0	0.67	0	0	0	1	
Cercocebus torquatus	0	0	0	0	0	0.67	0	1	0	1	
Cercopithecus campbelli	0	0	0	0	0	0.70	0	0	0	0	
Cercopithecus diana	0	0	0	0	0	0.69	0	0	0	0	
Cercopithecus mitis	0	0	0	0	0	0.68	0	0	0	0	
Chiropotes satanas	0	0	0	0	0	0.67	0	0	0	1	
Chlorocebus aethiops	0	0	0	0	0	0.69	0	1	0	1	
Colobus guereza	0	0	0	0	0	0.40	0	0	0	1	
Daubentonia madagascarensis	1	0	0	0	2	0.84	0	0	0	0	47-49
Erythrocebus patas	0	0	0	0	0	0.69	0	0	0	0	
Eulemur fulvus	0	0	0	0	0	0.59	0	0	0	1	
Eulemur rufus	0	0	0	0	0	0.59	0	0	0	1	
Galago senegalensis	1	0	0	0	0	0.63	0	0	0	0	50,51
Gorilla beringei	1	0	0	0	1	0.34	0	0	0	0	52
Gorilla gorilla	1	0	0	0	1	0.38	0	0	0	0	53
Hylobates lar	1	0	0	0	0	0.71	0	0	1	0	54-59
Indri indri	0	0	0	0	0	0.55	0	0	1	0	
Lemur catta	0	0	0	0	0	0.59	0	0	0	1	
Leontopithecus rosalia	2	0	0	1	1	0.67	0	0	1	1	60-70

Species										
Lophocebus albigena	0	0	0	0	0	0.69	0	1	0	1	
Macaca arctoides	1	0	0	0	1	0.68	0	0	0	1	71
Macaca fascicularis	1	0	0	0	1	0.74	1	1	0	1	72,73
Macaca fuscata	1	0	0	0	1	0.68	0	1	0	1	74,75
Macaca mulatta	0	0	0	0	1	0.68	0	1	0	1	
Macaca nemestrina	0	0	0	0	1	0.62	0	1	0	1	
Macaca radiata	0	0	0	0	1	0.68	1	0	0	1	
Macaca silenus	0	0	0	0	1	0.68	0	0	0	1	
Macaca sylvanus	0	0	0	0	1	0.68	1	0	0	1	
Mandrillus sphinx	0	0	0	0	0	0.67	0	0	0	1	
Microcebus murinus	0	0	0	0	0	0.76	0	0	0	0	
Nasalis larvatus	0	0	0	0	0	0.53	0	0	0	1	
Nomascus concolor	1	0	1	0	0	0.43	0	0	1	0	76
Nycticebus coucang	1	0	0	0	0	0.79	0	0	1	0	77
Pan paniscus	2	1	1	1	2	0.61	0	1	0	1	78-87
Pan troglodytes	2	1	1	1	2	0.61	1	1	0	1	88-136
Papio anubis	1	0	0	1	1	0.66	1	0	0	1	137-139
Papio cynocephalus	0	0	0	0	1	0.65	0	0	0	1	
Papio hamadryas	0	0	0	0	1	0.66	0	0	0	1	
Papio ursinus	0	0	0	0	1	0.63	0	0	0	1	
Piliocolobus badius	1	0	0	0	0	0.40	1	0	0	1	140
Pithecia pithecia	1	1	0	0	0	0.67	0	0	0	0	141
Pongo abelii	2	0	1	1	2	0.59	0	0	0	1	142-144
Pongo pygmaeus	2	0	1	1	2	0.59	0	0	0	1	
Presbytis thomasi	0	0	0	0	0	0.55	0	0	0	0	
Propithecus verreauxi	0	0	0	0	0	0.56	0	0	0	1	
Pygathrix nemaeus	1	0	1	1	0	0.54	0	0	0	1	145
Saguinus fuscicollis	2	1	0	0	0	0.67	0	0	1	1	146-148
Saguinus mystax	2	0	0	1	0	0.67	0	0	1	1	149,150
Saguinus nigricollis	2	0	0	0	0	0.67	0	0	1	1	151

Species											Ref.
Saguinus oedipus	2	0	0	0	0	0.67	0	0	1	1	152-163
Saimiri sciureus	0	0	0	0	1	0.94	0	1	0	1	164,165
Semnopithecus entellus	1	0	0	0	0	0.42	0	0	0	1	166
Symphalangus syndactilus	1	0	0	0	0	0.49	0	0	1	0	167
Tarsius tarsier	1	0	0	0	0	1.00	0	0	1	0	168
Theropithecus gelada	0	0	0	0	0	0.40	0	1	0	1	

[a]Species names follow Groves (2001) and Brandon-Jones et al. (2004)

[b]Ref. = References for food sharing information.

FS = Food sharing, with infants (inf.) among adults (ad.), among males (♂-♂), among females (♀-♀) and from males to females (♂-♀) respectively. Diff. = difficulty, DQI = Diet quality index, Monog. = Monogamy, ♀ choice = Opportunity for female choice

References: [1-4]Carpenter (1934; 1965), Baldwin & Baldwin (1973), Whitehead (1986); [5-7]Wolovich et al. (2006; 2008a; 2008b); [8-10]Dare (1974), Watt (1994), Pastor-Nieto (2001); [11,12]Fragaszy & Mason (1983), Wright (1984); [13]Starin (1978); [14-17]Lorenz (1969; 1972), Feistner & Price (1991), Jurke & Price (1994); [18-20]Carroll (1978), Omedes (1981), Feistner & Price (1991); [21-32]Epple (1967), Hearn & Lunn (1975), Chalmers & Lockehaydon (1984), Feistner & Price (1991), Vitale & Queyras (1997), Yamamoto & Box (1997), Westlund et al. (2000), Caldwell & Whiten (2003), Brown et al. (2005), de Lyra-Neves et al. (2007), Kasper et al. (2008), Saito et al. (2008); [33,34]Christen (1968), Feistner & Price (1991); [35]M. van Noordwijk & C. van Schaik (unpubl. data); [36-43]Thierry et al. (1989), de Waal et al. (1993)f, Fragaszy et al. (1997; 2004), Westergaard & Suomi (1997), Westergaard et al. (1998; 1999), de Waal (2000); [44-46]Perry & Rose (1994), Rose (1997; 2001); [47-49]Feistner & Ashbourne (1994), Winn (1994), Krakauer & van Schaik (2005); [50,51]Nash (1991; 1993); [52]Watts (1985); [53]Nowell & Fletcher (2006); [54-59]Carpenter (1940), Berkson & Schusterman (1964), Ellefson (1968), Fox (1972), Shessler & Nash (1977), Nettelbeck (1998); [60-70]Wilson (1976), Brown & Mack (1978), Hoage (1982), Price & Feistner (1993), Rapaport (1999; 2001; 2006b), Ruiz-Miranda et al. (1999), Rapaport & Ruiz-Miranda (2002; 2006), Tardif et al. (2002); [71]Bertrand (1969); [72,73]Kummer & Cords (1991), M. van Noordwijk (pers.comm.); [74,75]Hikami et al. (1990), Matusbara & Funakoshi (2001); [76]Fan & Jiang (2009); [77]Zimmermann (1989); [78-87]Kano (1980), Badrian & Badrian (1984), Badrian & Malenky (1984), Kuroda (1984), de Waal (1992), Hohmann & Fruth (1993; 2008), White (1994), Fruth & Hohmann (2002), Surbeck & Hohmann (2008), Jaeggi et al. (2010b); [88-136]Nissen & Crawford (1936), van Lawick-Goodall (1968), Nishida (1970; 1983), Suzuki (1971), Teleki (1973), McGrew (1975), Wragham (1975), Silk (1978; 1979), Nishida et al. (1979; 1992), Tutin (1979), Kawanaka (1982), Takahata et al. (1984), Goodall (1986), Boesch & Boesch-Achermann (1989; 2000), de Waal (1989; 1992; 1997), Hiraiwa-Hasegawa (1990b; 1990a), Boesch (1994), Kuroda et al. (1996), Nishida & Turner (1996), Hemelrijk et al. (1999), Mitani & Watts (1999; 2001), Newton-Fisher (1999), Stanford (1999), Bethell et al. (2000), Nakamura & Itoh (2001), Hunt & McGrew (2002), Matsumoto-Oda (2002), Watts & Mitani (2002), Hirata & Celli (2003a), Ueno & Matsuzawa (2004), Stevens (2004), Reynolds (2005), Slocombe & Newton-Fisher (2005), Gilby (2006), Lonsdorf (2006), Mitani (2006), Hockings et al. (2007), Pruetz & Bertolani (2007), Gomes & Boesch (2009), Jaeggi et al. (2010b), Gilby et al. (in press); [137-139]Harding (1973), Strum (1975; 1981); [140]Starin (2006); [141]Homburg (1997); [142-144]Utami & van Hooff (1997), van Noordwijk & van Schaik (2009), Forss et al. (2009); [137-141]Horr (1977), Bard (1987; 1992), Jaeggi et al. (2008), van Noordwijk & van Schaik (2009); [145]Kavanagh (1972); [146-148]Cebul & Epple (1984), Yoneda (1984), Goldizen (1989); [149,150]Heymann (1996), Huck et al. (2004); [151]Izawa (1978); [152-163]Wolters (1978), Neyman (1980), Cleveland & Snowdon (1984), Feistner & Chamove (1986), Feistner & Price (1990; 1991; 1999), Savage et al. (1996), Roush & Snowdon (2000; 2001), Joyce & Snowdon (2007), Humle & Snowdon (2008b); [164,165]Fragaszy & Mason (1983), Stevens (2004); [166]Jay (1965); [167]Fox (1972); [168]Gursky (2000)

Comparative analyses

We used both maximum likelihood and Bayesian approaches to test for correlated evolution of the traits of interest while controlling for phylogenetic dependence. The phylogeny of primates was based on Bininda-Emonds et al. (2007). An overview of all the tests and the support for the relevant hypotheses is given in Table 1-3. First, we fitted regression models using phylogenetic generalized least squares (PGLS) for continuous traits and generalized estimating equations (GEE) for discrete traits (Paradis 2006), which are both based on restricted maximum likelihood. Models were fitted using the ape package (Paradis et al. 2009) in R 2.9.0 (R Development Core Team 2009) and we report parameter estimates and their P values.

Second, for discrete traits we also used reversible-jump Markov chain Monte Carlo (RJ MCMC) to estimate parameters from a posterior distribution (Pagel and Meade 2006) using BayesTraits 1.0 (Pagel and Meade) with a burn-in of 50,000 and 5,050,000 iterations in total. Prior settings were the same as in Pagel and Meade (2006). RJ MCMCs are used to model the evolution of two discrete traits assuming either dependent or independent evolution (the latter being the null hypothesis). Similar to a likelihood-ratio test, the two models are compared by their harmonic means, the Bayesian equivalent of the log-likelihood, by calculating the log Bayes factor (BF). Rather than testing the BF against a distribution, by convention, a BF >2 is taken as positive evidence for dependent evolution, BF >5 as strong positive evidence and BF >10 as very strong positive evidence (Pagel and Meade 2006). Furthermore, even in the dependent model, the chain can visit models with independent evolution in proportion to their posterior probabilities. Thus, if the proportion of independent models visited,

$P_{independent}$, is small, the null hypothesis of independent evolution of the two traits can be rejected. We report both the BF and $P_{independent}$ for each model.

In addition, RJ MCMC can be used to calculate the probabilities for trait changes, so-called "rate parameters" (Pagel and Meade 2006). If two traits can have the states (0,0), (0,1), (1,0) or (1,1), the rate parameters refer to the probability of transition between these states (Figure 1-1). Hence, one can test whether the evolution of one trait, e.g. "sharing among adults", is more likely in the presence or the absence of the other trait, e.g. "sharing with infants", by comparing q_{24} (transition from (0,1) to (1,1)) with q_{13} (i.e. the transition from (0,0) to (1,0)). If q_{24} is different from q_{13}, there is evidence for correlated evolution of the two traits. For a graphical examination of this, one can plot the posterior distribution of rate parameters simulated by the RJ MCMC (cf. Appendix 1-1). Furthermore, one can use the estimated rate parameters to graphically indicate the likely evolutionary routes of state transitions in a flow chart by modifying the thickness of the arrows accordingly (cf. Figure 1-4).
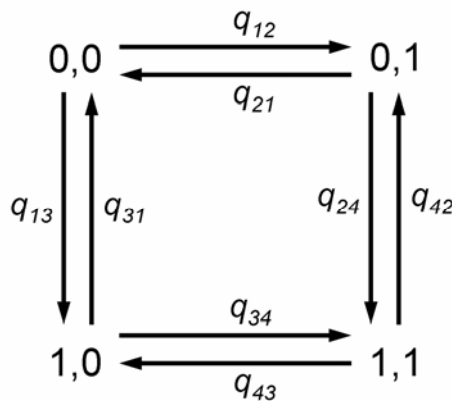
Figure 1-1: Redrawn from Pagel and Meade (2006, Figure 7): Transitions among the four possible combinations of states resulting from two binary variables. Subscripts identify the beginning and ending states of each transition, where the values 1, 2, 3, and 4 correspond to the state pairs (0,0), (0,1), (1,0), and (1,1). Thus, q_{12} describes the transition between state (0,0) and state (0,1)

Results

General patterns

Of the 68 species in the sample, in 38 (55.9%) food was shared with infants. In no species food was shared among adults but not with infants. Of those 38 species in which food was shared with infants, in 17 (44.7%) food was also shared among adults. In particular, in 14 species males shared with females and males and females shared among themselves in seven species each. This distribution of sharing among adults in relation to the presence of sharing with infants and measures for valuable relationships is summarized in Table 1-2. Fisher's exact probabilities indicate that these variables are significantly associated, except for monogamy.

Table 1-2: Contingency Table showing the distribution of species across food sharing and valuable relationship categories and Fisher's exact tests for the association of these variables

		Sharing w. inf.		Female choice		Monogamy		♂-♂ coalitions		♀-♀ coalitions	
		1	*0*	*1*	*0*	*1*	*0*	*1*	*0*	*1*	*0*
Sharing	*1*	17	0	12	2	5	9	4	3	3	4
ad.	*0*	21	30	11	13	12	12	4	27	2	29
Fisher's exact		P<0.001		P<0.05		P=0.51		P<0.05		P<0.05	

Note that the first column, sharing with infants (sharing w. inf.), refers to the whole sample (68 species) and any dyad sharing among adults (Sharing ad.) whereas the other columns refer to the restricted sample of those species already sharing with infants (38 species) and to particular dyads related to the respective measure of valuable relationships, i.e. sharing from males to females for female choice and monogamy, as well as sharing among males or females for male-male (♂-♂) and female-female (♀-♀) coalitions respectively

Sharing with infants

The parameter estimates of the PGLS for sharing with infants are given in Table 1-3. Neither diet quality nor diet difficulty had a significant influence on sharing with infants. However, diet quality had a negative influence on sharing suggesting that the nutritional hypothesis was not supported. Diet difficulty had a slight positive influence, thus hinting at a mild support of the informational hypothesis (Figure 1-2).

a)   b)
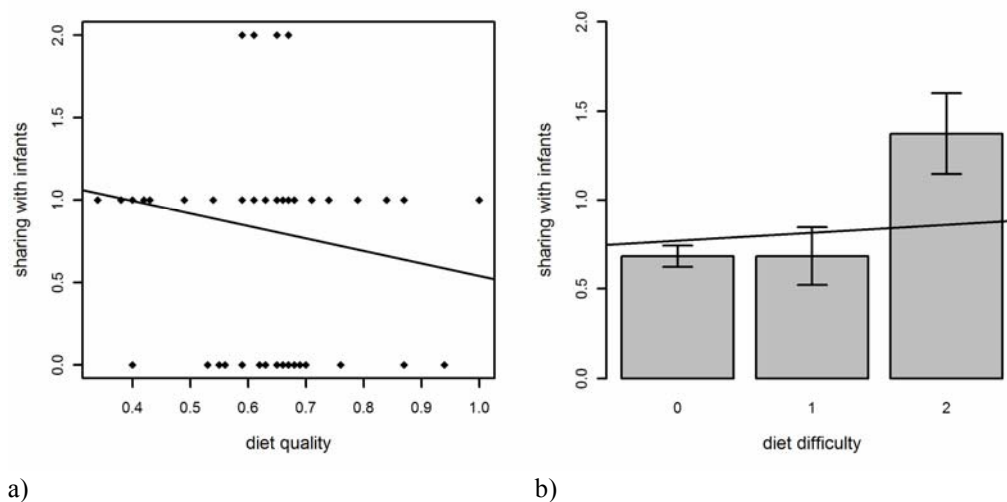
Figure 1-2: Food sharing with infants as a function of a) diet quality and b) diet difficulty. The plotted lines represent the estimated regression line from phylogenetic generalized least squares models. Error bars represent standard deviations

Sharing among adults

Species sharing among adults represented a strict subset of those species sharing with infants (Table 1-2). Thus, sharing with infants had a highly significant positive influence on sharing among adults (PGLS, see Table 1-3 for parameter estimates). Furthermore, the RJ MCMC provided very strong support for dependent evolution of

the two traits: the log Bayes factor, comparing the harmonic means of the dependent

and the independent model, was very high and the chain never (!) visited independent

evolution (see Table 1-3 for a summary of these results). The posterior distribution of

rate parameters is given in Appendix 1-1 and also strongly indicated dependent

evolution (compare e.g. q_{13} vs. q_{24} for probability for gain of sharing among adults in

absence or presence of sharing with infants).

Thus, sharing with infants can be seen as a necessary precondition for sharing

among adults. Hence, in order to further test what factors explain sharing among

specific dyads of adults, we reduced our data set to species already sharing with infants

(N=38).

From males to females Sharing from males to females was significantly positively

predicted by the opportunity for female choice (GEE: $F_{1,38}$=6.53, P<0.05, Table 1-3),

but not by the presence of monogamy (GEE: $F_{1,38}$=0.08, P=0.79, Table 1-3). Similarly,

the RJ MCMC provided positive evidence for dependent evolution of sharing from

males to females and the opportunity for female choice, but not for monogamy, even

though the chain did not visit a significant number of independent models (Table 1-3).

The posterior distributions of rate parameter also indicated dependent evolution

(Appendix 1-1). Hence the female mate choice hypothesis for the evolution of sharing

from males to females was supported (Figure 1-3a) whereas the pair-bonds hypothesis

was not supported.

Among males The presence of male-male coalitions significantly explained sharing

among males (GEE: $F_{1,38}$=6.15, P<0.05, Table 1-3) and the RJ MCMC also provided

strong support for dependent evolution (Table 1-3). The posterior distributions of rate

parameter also indicated dependent evolution (Appendix 1-1). Hence the valuable

relationships hypothesis for male-male sharing was supported (Figure 1-3b).

<u>Among females</u> Female-female coalitions significantly predicted sharing among

females (GEE: $F_{1,38}$=7.91, P<0.05, Table 1-3) and the RJ MCMC provided strong

Table 1-3: Overview of the comparative analyses, the factors included in the models and the related hypotheses

Food Sharing	N	Factors	PGLS/GEE[a]	RJ MCMC[b]	Related Hypotheses	Supported?
with infants	68	*Intercept*	1.40			
		Diet difficulty	0.10		Informational hypothesis	(+)
		Diet quality	-0.93		Nutritional hypothesis	(-)
among adults (any dyad)	68	*Intercept*	-0.44			
		Sharing with infants	0.77***	$P_{ind.}$=0, BF=30.73	Derived behavior	+++
from males to females[c]	38	*Intercept*	-1.87			
		Female choice	1.96*	$P_{ind.}$=0.004, BF=3.56	Female mate choice ("Food-for-sex")	+
		Intercept	0.29			
		Monogamy	-0.58	$P_{ind.}$=0.03, BF=1.11	Pair-bonds	-
among males[c]	38	*Intercept*	-2.20			
		Male-male coalitions	2.2*	$P_{ind.}$=0.001, BF=6.29	Coalition partners ("Food-for-support")	++
among females[c]	38	*Intercept*	-1.98			
		Female-female coalitions	2.39*	$P_{ind.}$=0.001, BF=5.63	Coalition partners ("Food-for-support")	++

[a]PGLS: Phylogenetic Generalized Least Squares. GEE: Generalized Estimating Equations. PGLS are used for continuous variables, GEE for discrete variables. Reported are the parameter estimates with significance
[b]RJ MCMC: Reversible-jump Markov chain Monte Carlo. Reported are the proportion of models that visited independent evolution of the traits, indicated by the probability for independent evolution $P_{independent}$, as well as the log Bayes-Factor (BF), which measures the fit of the dependent model relative to the independent model. By convention, a BF > 2 is taken as positive evidence for dependent evolution, >5 indicates strong positive evidence and >10 very strong positive evidence
[c]Only species sharing with infants
***: P<0.001, *: P<0.05

evidence for dependent evolution (Table 1-3). The posterior distributions of rate

parameter also indicated dependent evolution (Appendix 1-1). Hence the valuable

relationships hypothesis for female-female sharing was supported (Figure 1-3c).

a)   b)   c)
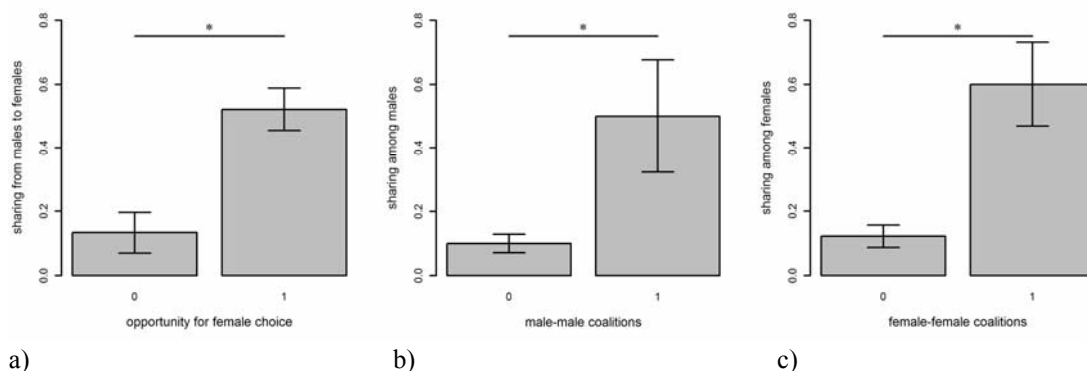
Figure 1-3: Mean (± SEM) species values for food sharing a) from males to females, b) among males and c) among females, in the absence (0) or presence (1) of a) the opportunity for female choice, b) male-male coalitions and c) female-female coalitions. The significance values (*: P<0.05) refer to the parameter estimates of the generalized estimating equations models (Table 1-3)

In sum, sharing with infants could not be fully explained, but was itself a

necessary precondition for the evolution of sharing among adults, thus providing

support to the derived-behavior hypothesis. Among particular dyads of adults, three

measures of valuable relationships showed evidence for correlated evolution with

sharing, thus supporting the valuable relationships hypothesis. This is summarized in

Figure 1-4, which shows the probabilities for evolutionary gains of the trait "sharing

among adults" in relation to the presence or absence of these other traits. It can be seen

that sharing among adults is much more likely to evolve if sharing with infants is

already present as a trait and that sharing among particular dyads of adults is more

likely to evolve in the presence of valuable relationships and vice versa.

a)   b)
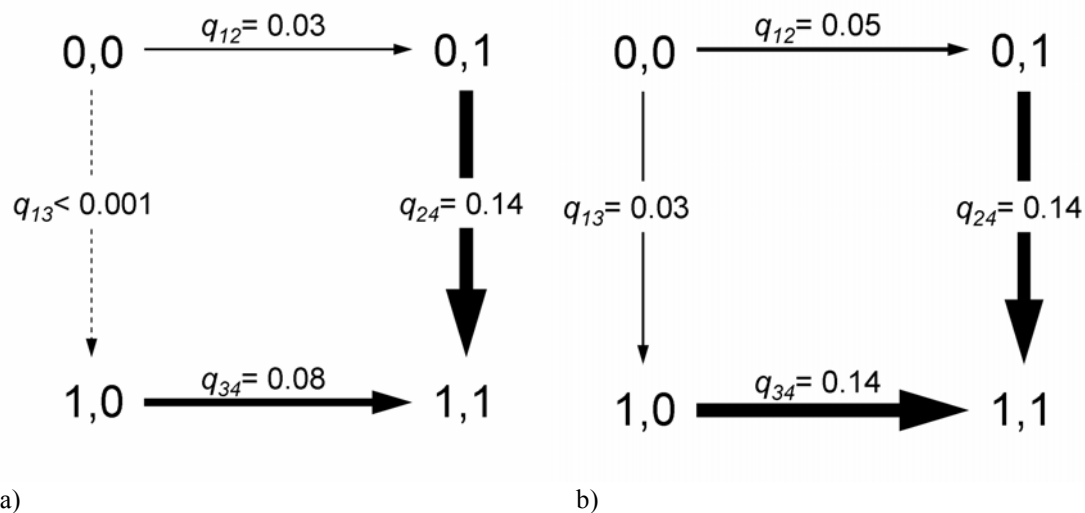
Figure 1-4: Flow charts for the evolution of food sharing among adults (first trait) and a) food sharing with infants or b) valuable relationships (second traits). Thus, (0,0) refers to absence of both traits, (0,1) is only a) sharing with infants or b) valuable relationships, (1,0) only sharing among adults and (1,1) sharing among adults and a) sharing with infants or b) valuable relationships. The thickness of the arrows is proportional to the values of q and thus to the probability of the transition from one state to another. The q-values in b) are the means of the dyad-specific analyses, i.e. male-female, male-male and female-female sharing, and female choice, male-male coalitions and female-female coalitions respectively (see Appendix 1-1 for full details). By comparing the rate pair q_{24} and q_{13} it can be clearly seen that the evolution of sharing among adults is much more likely if a) sharing with infants or b) valuable relationships is already present as a trait. Note that a) is based on 68 species while b) is based on only 38 species, namely those in which sharing with infants was already present

Discussion

Valuable relationships are characterized by strong social tolerance and the reciprocal exchange of prosocial acts (Silk 2002; Silk 2006). Sharing of food among primates is predominantly passive (Brown et al. 2004; Jaeggi et al. in press) and thus in its most basic form, allowing another individual to take food is simply a display of such

tolerance towards a valuable social partner (van Noordwijk and van Schaik 2009). Since owners are often dominant over beggars, including instances of sharing from males to females, this displayed tolerance can be seen as a result of subordinate leverage (Lewis 2002). Repeated such interactions will lead to reciprocal patterns in which, depending on balance or bias of ownership, sharing will be traded for itself or for other currencies such as matings or agonistic support. Thus, we summarized hypotheses explaining sharing by reciprocity as the *valuable relationships hypothesis* and found strong support for it in this comparative study: the evolution of sharing and valuable relationships, as measured by the opportunity for female mate choice as well as male-male and female-female coalitions, were clearly linked (Figures 1-3 & 1-4b).

Sharing among adults only evolved in a subset of the species, namely those in which sharing with infants had already been established (Figure 1-4a). The latter can therefore be seen as derived behavior (Tinbergen 1952), which could be pressed into service in another context. Such constraints on the evolution of potentially adaptive behaviors may be quite common (Ryan 2009). Thus, some behaviors can only evolve when their precursor is already in place, even if all the conditions favoring its occurrence are met in principle. Hence, in some species of primates where valuable relationships occur, sharing among adults may remain absent because its precursor sharing with infants is lacking (Tables 1-1 & 1-2). In these species the high tolerance emerging from valuable relationships may be displayed by other behaviors such as grooming or play.

Conversely, some species showed sharing within particular dyads in the absence of the respective measure for valuable relationships (Figure 1-3, Table 1-1 & 1-2). This could be explained by the evolution of high social tolerance for other reasons in these

species. For instance, sharing among males in the absence of male-male coalitions occurs among bonobos *Pan paniscus*, saddleback tamarins *Saguinus fuscicollis* and white-faced sakis *Pithecia pithecia* (Table 1-1). In bonobos, sharing among males is actually much rarer than in any other dyad (Kuroda 1984; Jaeggi et al. 2010b), as expected from the absence of coalitions, and does not seem to serve an adaptive function. In the other two species, sharing among males may be a consequence of polyandry (*Saguinus fuscicollis*: Goldizen 1989; *Pithecia pithecia*: Homburg 1997), as mentioned above. In the case of female-female sharing, the orangutans *Pongo abelii* and *Pongo pygmaeus*, douc langurs *Pygathrix nemaeus* and black crested gibbons *Nomascus concolor* are the exceptions. The latter may be due to polygyny (Fan and Jiang 2009), the former due to other forms of cooperation not commonly scored as coalitions (M. van Noordwijk et al. in prep.).

Another possible constraint on the evolution of sharing (and valuable relationships) is the dominance structure of a group which may restrict both the owner's ability to share selectively with valuable partners as well as the partners ability to selectively provide the service: Only in relatively egalitarian groups can services be exchanged reciprocally, whereas in despotic groups dominant individuals can acquire desired goods by force, thus destroying the market (Trivers 1971; Noë and Hammerstein 1994; Jaeggi et al. 2010b). Hence, a despotic dominance structure may reduce the number of species in which sharing with valuable partners could potentially evolve.

This "despotism constraint" may explain why in some highly despotic species, such as yellow baboons *Papio anubis*, sharing among males is absent despite the presence of male-male coalitions. The most dominant males can usually acquire food by

force (Strum 1975; Strum 1981) but do not need to form coalitions (Noë and Sluijter 1995), obviating the opportunity for an exchange of food for support (Trivers 1971). Similar arguments can be made for the despotism constraint on food-for-support among females or the female mate choice hypothesis.

Finally, the attractiveness of the diet of a given species may also constrain the evolution of sharing (Moore 1984). However, species sharing among adults is not a subset of any diet category (Table 1-1) and thus diet attractiveness is probably not a strong precondition for sharing among adults. Seeing that sometimes relatively low-quality and ubiquitous food is shared (Slocombe and Newton-Fisher 2005; van Noordwijk and van Schaik 2009) the social benefits of sharing may be achieved regardless of the food item at stake. This can also be seen in species that probably do not share food often in the wild but did evolve high social tolerance, which can lead to sharing given the right conditions in captivity (e.g. Berkson and Schusterman 1964; Kavanagh 1972; Schessler and Nash 1977; Zhang et al. 2008). Hence, we predict that any species that evolved valuable relationships should share food given the right conditions, and given that they also share with infants. If sharing among adults can be induced even in the absence of sharing with infants in the species, the behavioral constraint may only apply to natural conditions.

For instance, many species of Asian colobines live in modular societies, where one-male units (OMU's) are surrounded by other OMU's and bachelor males (Yeager and Kirkpatrick 1998; Grueter and van Schaik 2009). This constant presence of other males, and hence the opportunity for female choice, led to high tolerance from males to females within a OMU as expressed by higher rates of male-female grooming, compared to non-modular species (Grueter 2009). Asian colobines thus present a good

taxon to further test the female mate choice hypothesis, with modular species predicted to share food more than non-modular ones. Other species living in modular societies, such as Geladas *Theropithecus gelada* or Hamadryas baboons *Papio hamadryas* may have evolved the same kind of within OMU cohesion that may be expressed in sharing under captive conditions. Furthermore, species with high levels of cooperation among males, such as *Ateles geoffroyi* (Aureli et al. 2006) or *Cacajao calvus* (Bowler and Bodmer 2009), should have evolved strong bonds among those males potentially expressed in sharing. Simple experiments using monopolizable food in captivity (de Waal 1989; Jaeggi et al. 2010b) could be used to test these hypotheses.

We did not find significant support for either hypothesis explaining sharing with infants. This may be due to the relative crudeness of our diet quality and difficulty measurements, as is inevitable for comparative analyses, or it may reflect a strong phylogenetic effect on the traits. For instance, all callithrichids may share food extensively regardless of the current difficulty or quality of their diet because their ancestors evolved to give birth to fast-growing twins, the energetic demands of which a mother alone cannot cover (Brown et al. 2004). Nonetheless, in an analysis of the species values, without controlling for phylogeny, diet difficulty positively predicted sharing with infants with a statistical trend (results not shown). Hence, as indicated by Figure 1-2, we suggest mild support for the informational hypothesis, while the nutritional hypothesis was probably not supported.

We also did not find support for the pair-bonds hypothesis, probably because sharing was too rare among monogamous species in the sample (5/17= 29%, Table 1-2). A sample with different groups of species, e.g. birds, might yield different results. The fact that the proportion of independent models visited by the chain of the RJ MCMC,

Pindependent, did support dependent evolution whereas the log Bayes factor and the posterior distributions of rate parameters did not, might suggest that Pindependent tends to be an underestimation of the probability for independent evolution and should thus not be used for hypothesis-testing or at least be taken with caution.

In sum, we conclude that the necessity to form valuable relationships, within which prosocial acts may be exchanged reciprocally, led to the evolution of high social tolerance and subordinate leverage among primates. In some species where sharing with infants was already present, this behavior was derived to perform social functions among adults, or in other words, the high social tolerance within valuable relationships was now also expressed in sharing, leading to reciprocal sharing patterns. Possible constraints on the evolution of sharing include despotism and, probably to a lesser extent, the attractiveness of the diet. Humans, throughout most of their evolutionary history, thus probably fulfilled all preconditions for the evolution of extensive sharing among adults: relatively egalitarian societies, highly attractive diets, provisioning of infants, female mate choice, pair bonds and coalitions both among males and among females (Woodburn 1982; Harcourt and de Waal 1992; Boehm 1999; Pandit and van Schaik 2003; Gurven 2004; Gurven and Hill 2009). Constraints on sharing such as despotism and increased monopolizability of resources may have re-emerged in more recent stages of human history (Kaplan et al. 2009).

Chapter 2: Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees

Tolerant food sharing among human foragers can largely be explained by reciprocity. In contrast, food sharing among chimpanzees and bonobos may not always reflect reciprocity, which could be explained by different dominance styles: in egalitarian societies reciprocity is expressed freely, while in more despotic groups dominants may hinder reciprocity. We tested the degree of reciprocity and the influence of dominance on food sharing among chimpanzees and bonobos in two captive groups. First, we found that chimpanzees shared more frequently, more tolerantly, and more actively than bonobos. Second, among chimpanzees, food received was the best predictor of food shared, indicating reciprocal exchange, whereas among bonobos transfers were mostly uni-directional. Third, chimpanzees had a shallower and less linear dominance hierarchy, indicating that they were less despotic than bonobos. This suggests that the tolerant and reciprocal sharing found in chimpanzees, but not bonobos, was made possible by the absence of despotism. To investigate this further we tested the relationship between despotism and reciprocity in grooming using data from an additional 5 groups and 5 different study periods on the main groups. The results show that (i) all chimpanzee groups were less despotic and groomed more reciprocally than bonobo groups, and (ii) there was a general negative correlation between despotism and

grooming reciprocity across species. This indicates that an egalitarian hierarchy may be more common in chimpanzees, at least in captivity, thus fostering reciprocal exchange. We conclude that a shallow dominance hierarchy was a necessary precondition for the evolution of human-like reciprocal food sharing.

Introduction

Extensive food sharing is universal among human foragers and has received considerable attention as a model for the evolution of altruistic behavior (Gurven 2004). Ultimately, food sharing among unrelated humans can be explained by tolerated scrounging (Blurton Jones 1984) and/or some form of direct or indirect reciprocity (Trivers 1971; Alexander 1987). The relative importance of the two models depends on the degree of control producers have over food distribution: if this control is high, reciprocal sharing patterns are more likely (Gurven 2004). Proximately, voluntary food sharing reflects high levels of prosociality which have probably co-evolved with reciprocity (Trivers 1971; Trivers 2006). Food sharing is also universal in *Pan*, having been reported from every major study site of both chimpanzees and bonobos (see Table 2-1). How then is food sharing regulated among our closest living relatives?

Table 2-1: Reported food sharing among adults of well studied chimpanzee and bonobo populations with main references

Species	Study Site
Chimpanzees *Pan troglodytes*	Bossou (only plant food)[1] Budongo[2,3] Gombe[4-11] Mahale[12-18] Ngogo[19-21] Taï[22-24]
Bonobos *Pan paniscus*	Lomako[25-27] Lui Kotale[28,29] Wamba (only plant food)[30,31]

[1](Hockings et al. 2007); [2,3](Suzuki 1971; Reynolds 2005); [4-11](van Lawick-Goodall 1968; Teleki 1973; Wrangham 1975; Tutin 1979; Goodall 1986; Stanford 1999; Gilby 2006; Gilby et al. in press); [12-18](Nishida 1970; Suzuki 1971; Nishida et al. 1979; Kawanaka 1982; Takahata et al. 1984; Nishida et al. 1992; Hosaka et al. 2001); [19-21](Mitani and Watts 2001; Watts and Mitani 2002; Mitani 2006); [22-24](Boesch and Boesch 1989; Boesch 1994; Gomes and Boesch 2009); [25-27](Hohmann and Fruth 1993; White 1994; Fruth and Hohmann 2002); [28,29](Hohmann and Fruth 2008; Surbeck and Hohmann 2008); [30,31](Kano 1980; Kuroda 1984)

As for human food sharing, two main hypotheses have been put forward to explain the function of food transfers among non-human primates: reciprocal exchange and sharing-under-pressure. Food represents a commodity that can be traded for itself or other commodities such as grooming, sex or support on a biological market (Noë and Hammerstein 1994). Such *reciprocal exchange* of food has been reported from a variety of different species including capuchin monkeys (de Waal 2000) and chimpanzees (de Waal 1989; de Waal 1997; Mitani and Watts 2001; Mitani 2006; Gomes and Boesch 2009), but only limited support has been found in bonobos (Fruth and Hohmann 2002). Lack of reciprocity may be explained by transfers being forced rather than tolerated: as Noë and Hammerstein (1994, p.1) pointed out, "market forces cannot function if it is possible to appropriate desired commodities without the consent of the owner". In this case, food transfers may be better described as *sharing-under-pressure* (Wrangham 1975). This hypothesis, which was formalized in a model by Blurton Jones (1984) and later Stevens and Stephens (2002), proposes that food owners may relinquish (part of)

their food if the costs of defending it are higher than the benefits of consuming it. This model has been shown to explain food transfers among some groups of chimpanzees and bonobos, as transfers increased with increasing harassment (Fruth and Hohmann 2002; Gilby 2006). However, as Stevens and Gilby (2004) and Gilby (2006) have pointed out, the two hypotheses are not mutually exclusive. Reciprocal sharing patterns may still emerge if food owners can retain control over food distribution, despite the costs inflicted by harassment, and selectively relinquish food to particular individuals, e.g. those who relinquished food to them in the past (see also Moore 1984). Thus the amount of reciprocal exchange possible is determined by the amount of control owners can exert over food distribution, which depends on the costs of defending food. Here we suggest that these costs, and thus the opportunity for reciprocal exchange, depend on the dominance structure of the population. When dominance hierarchy is steep, dominants can monopolise resources or commodities and there is no reciprocal exchange. In the words of Trivers (1971), "strong dominance hierarchies reduce the extent to which … the less dominant individual is capable of performing a benefit for the more dominant *which the more dominant individual could not simply take at will*" (p. 38, emphasis added).

Proximately, the degree of prosociality in food sharing may be measured by the reactions of food owners to approaches and the way in which food is transferred (Jaeggi et al. in press). Thus, positive reactions to approaches and tolerant sharing would reflect more prosociality than negative reactions and forced transfers. Among chimpanzees, food transfers can vary from relatively active to mainly passive, reluctant or even aggressive (e.g. Teleki 1973; Boesch and Boesch 1989; Gilby 2006), but no formal hypotheses have been put forward to explain differences in sharing patterns between

populations. Similar differences probably exist among bonobos although data are scarcer and harder to compare because of different food types being shared (sugar cane (Kuroda 1984), large fruits (White 1994) and/or meat (Fruth and Hohmann 2002)). In the only study thus far directly comparing food sharing in the two species, de Waal (1992) found that chimpanzees shared more tolerantly, but he did not offer an ultimate explanation. Following Trivers (1971; 2006), we suggest that the psychological regulations of food sharing may ultimately depend on a history of reciprocity: only if food owners can expect to be reciprocated in some form should they voluntarily give away food. Conversely, more voluntary or active forms of sharing may induce more feelings of gratitude in the recipient, because they reflect genuine altruistic dispositions, and are thus reciprocated better (Trivers 1971). We therefore hypothesize that both the ultimate and the proximate mechanisms for sharing food will be influenced by the dominance structure of a group. The latter determines the costs of defending food and thus the amount of control owners have over food distribution, which in turn determines how much reciprocal exchange and tolerant sharing is possible.

Dominance hierarchies in primate societies can be characterized as ranging from egalitarian to despotic (van Schaik 1989) which has been formalized in terms of linearity and steepness of the hierarchy (de Vries 1995; de Vries et al. 2006). The steepness of the hierarchy is measured by the relative ability of group members to win dyadic conflicts: the steeper the hierarchy, the more easily dominants win conflicts with subordinates. Thus, in a group with a steep hierarchy, the costs of defending food should be high, owners cannot retain control over food distribution and transfers will be forced by dominants, which are unlikely to reciprocate. On the other hand, in a group with a shallow hierarchy, the costs of defending food should be low, owners can retain

control over food distribution and selectively tolerate transfers by those individuals who reciprocate. Once reciprocity is established, owners may also share food more actively.

Hierarchy steepness has also been shown to negatively influence reciprocity in *grooming* among captive bonobos (Stevens et al. 2005) and other primates (Schino and Aureli 2008), mostly because more grooming is directed up the hierarchy in despotic groups. This correlation has so far only been shown within species. To test whether a general relationship between despotism and reciprocity is consistent across the two species studied here, we compared hierarchy steepness and grooming reciprocity in 5 groups of chimpanzees and 8 groups of bonobos.

In sum, we predict that in egalitarian groups, food transfers will be tolerant and reciprocal while in despotic groups, transfers are forced and non-reciprocal. We tested these predictions by recording food interactions in one group of captive chimpanzees and bonobos respectively, and (i) describe general food sharing patterns, in particular the relative amount of forced and tolerated transfers, (ii) test what factors best explain the observed food transfers, in particular reciprocal exchange, and (iii) link the degree of tolerance and reciprocity to the degree of despotism. By studying these aspects in our two closest living relatives we hope to make inferences about the evolution of human food sharing and the proximate mechanisms linked to it.

Methods

Subjects and housing

The chimpanzees lived at the Abenteuerland Walter Zoo in Gossau SG, Switzerland (indoor enclosures: 2x 150m^2, outdoor enclosures: 2x 450m^2). The group

consisted of 11 adults and 2 infants, a third infant was born in the course of the study

and three of the 55 adult dyads were maternal relatives (see Appendix 2-1). None of the

females had regular swellings during the study. The bonobos lived at the Dierenpark

Planckendael, Belgium (indoor: 88m², outdoor: 3000m²). The group contained 6 adults

and 3 infants. Three of the 15 adult dyads were maternal relatives (Appendix 2-1). All

females were lactating and showed no regular swelling cycle. In both groups, only the

adults (minimum age 7) were subjects of this study.

Data collection

The chimpanzees were observed from October 2007 until February 2008 (Table

2-2). All occurrence observations on the whole group (Altmann 1974) took place

between approximately 9a.m. and 4p.m. on average two days a week, totaling 82h of

observation on all individuals. The bonobos were observed from 3rd of March to 5th of

May 2008 on five to six days a week between approximately 9a.m. and 5p.m., totaling

125h of observation on all individuals (Table 2-2). Observations on both groups

included all occurrences of social interactions, i.e. all grooming bouts (in sec.),

affiliative contact, dominance-, agonistic- and sexual interactions. In addition, proximity

scans recording each individuals distance to each other individual were taken every 5

minutes if the animals were not moving or feeding. The ethograms used were based on

van Hooff (1973) for the chimpanzees and on Vervaecke et al. (2000) for the bonobos.

Behaviors in both groups were recorded by AJ on paper or using live coding on InterAct

8.4.1.

Table 2-2: Details on study period and observers for each group. Capital letters indicate the study site, lower case letters indicate distinct groups at the same site (only GD) and numerical suffixes indicate the same group studied at different times (see Appendix 2-1 for details and changes in composition)

Species	Study Group	Study Period	Observers/Reference**
Chimpanzees	GD a1	Sep 2004 – Jan 2005	Peterhans (2006)
	GD a2	Jul – Oct 2006	Ziltener (2007)
	GD b	Sep 2004 – Jan 2005	Peterhans (2006)
	GS 1	Feb – May 2007	Ziltener (2007)
	GS 2*	**Oct 2007 – Feb 2008**	**this study**
Bonobos	A	Feb – Apr 2001	Stevens et al. (2005)
	P 1	1992 – 1993	Vervaecke et al. (2000)
	P 2	Nov – Dec 1999	Stevens et al. (2005)
	P 3	Nov 2002 – Feb 2003	Stevens et al. (2005)
	P 4	Feb - May 2006	Stevens et al. (2007a)
	P 5*	**Apr – May 2008**	**this study**
	T	Nov – Dec 2001, Feb 2002	Stevens et al. (2005)
	W	Aug – Sep 1999	Stevens et al. (2005)

* main study groups; others are additional groups only used for hierarchy steepness and grooming reciprocity analyses (Figure 2-3)
** Main observers were the first authors of the respective reference, except for Stevens et al. 2007, where the second author was the main observer. The methodology (ethogram, observation methods) was the same in all studies. Study sites: GD=Gänserndorf, GS=Gossau, A=Apenheul, P=Planckendael, T=Twycross, W=Wuppertal

Food-sharing experiments

Following de Waal (1989; 1997) we used monopolizable food sources to induce food interactions. We used paper shopping bags filled with part of the apes' regular diet, mostly vegetables. In the chimpanzee group, food-sharing experiments were conducted once a day, around 1-2p.m (N=30). In the bonobo group, experiments were conducted once or twice a day, in the morning, around 9-10a.m (N=28) and/or in the early afternoon, around 1-2p.m (N=25). For both species, the paper bags were either put in the indoor enclosure before the apes were let in, or thrown to specific individuals in the outdoor enclosure. In addition, spontaneous food interactions during normal feedings were recorded. All experiments were video-taped and all food interactions were

subsequently coded by AJ with InterAct 8.4.1. To test for inter-observer comparability of our food transfer definitions, JS also coded a sequence including different types of transfers among the chimpanzees, resulting in substantial agreement (K=0.63).

Food interactions. The food owner's reaction to each approach was classified as either *positive*, i.e. conducive to food transfer (give food to approacher, drop food in approacher's reach or hold food toward approacher), *negative*, i.e. impeding food transfer (protest vocally, hold on to food, hold away food, turn away, leave, flee, push away approacher's hand, attack approacher), or *neutral*, i.e. neither conducive to nor impeding food transfer (ignore approacher, other behavior). We defined food transfers like van Noordwijk & van Schaik (2009) as transfers out of the owner's hand. Following de Waal (1989; 1992) we distinguished between types of *non-tolerated transfers* and *tolerated transfers* (see Table 2-4 for operational definitions). Contrary to de Waal (1989; 1992) we did not observe *co-feeding* (due to the different food types) and did not include *collect near* in the analyses as this was never protested by food owners and ownership was thus not claimed. *Food-getting success* was defined as the proportion of approaches that led to food transfer.

On average (±SD), individual chimpanzees were first owner 2.8 ±2.6 times (range 0-8) and bonobos 8.8 ±5.6 (2-17) times. 564 and 640 approaches respectively were recorded and each possible owner-approacher dyad interacted on average (±SD) 6.3 ±13.2 (0-100) / 22 ±28.7 (0-121) times.

Additional groups

To compare general patterns of reciprocity and dominance across different groups of chimpanzees and bonobos we included data from an additional 5 groups (one

of which studied twice) and 5 different study periods on the main groups resulting in 5

and 8 samples per species (see Appendix 2-1 and Table 2-2 for details on composition

as well as observation periods and observers). To be included in this analysis, the data

had to fulfill two criteria: (i) the hierarchy steepness estimate had to be significant,

which was tested with a randomization test using 2000 repeats (de Vries et al. 2006) and

(ii) the grooming matrix correlation coefficient for any group of n individuals had to be

based on at least 2n(n-1) grooming bouts, thus allowing for each dyad to reciprocate at

least once.

Statistical analyses

　　　　To test the influence of various factors on food transfers we used generalized

linear mixed effects models (GLMM: Bolker et al. 2009), including the identities of

owner and approacher as random factors. For an overview and definitions of fixed

factors see Table 2-3 and below. GLMM's were fitted with lme4 (Bates and Maechler

2009) in R 2.9.0 (2009) with binomial error distribution. We first constructed a full

model, including all possible factors and tested the overall significance of the full model

against a null model, including only the intercept and the random factors (Johnson and

Omland 2004). We then used the corrected Akaike's Information Criterion (AICc:

Hurvich and Tsai 1989) to select the most parsimonious model with the best fit to the

data (Johnson and Omland 2004). Factors were excluded only if this improved the

model fit by >2 AICc units. This approach avoids the danger of increased type II errors

with repeated significance testing (Mundry and Nunn 2009). We used likelihood ratio

tests to test whether a full model or a factor of interest explained a significant amount of

the variance compared to the null model or a reduced model without the factor of

interest, respectively. Since likelihood ratio tests against a Chi-square distribution tend to overestimate effect size (Faraway 2006) we used parametric bootstrapping with 1000 Monte Carlo simulations to generate a distribution of likelihood ratios (LR) from the fitted parameter estimates and tested the observed LR against this distribution (Faraway 2006). In the case of borderline P values (0.05-0.1) we ran 10,000 simulations. Rowwise matrix correlations in MatMan (de Vries 1993) yielded very similar results, but since matrix correlations cannot handle multiple factors simultaneously we only report the results of the GLMM's.

 Dependent variables. We used two different measurements of food getting success as dependent variables. *Transfers given[1]:* Proportion of approaches that led to food transfer, both tolerated and forced, for a given owner-approacher dyad. *Tolerated transfers given*: Proportion of approaches that led to tolerated food transfer for a given owner-approacher dyad. Both measurements were weighted by the total number of approaches per dyad. Reciprocal exchange is mainly expected for tolerated transfers but may also occur over all transfers, if forced transfers are rare. The more common forced transfers, the weaker the signal of reciprocity over all transfers.

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[1] „Given" and "received" are only used to indicate the direction of transfers, from owner to approacher or vice versa, but do not imply intention or voluntariness

Table 2-3: Dependent variables included in the generalized linear mixed models to explain food transfers and hypotheses associated with them

Dependent variable	A shares with B because…	Hypothesis	Supported?[5]
(Tolerated) Transfers received	B shares with A	Reciprocity (food for food)	Chimpanzees yes, bonobos no
Relationship quality[1], affiliative relationship[2]	A and B are friends	Interchange (food for other services) / expression of tolerance	Yes
Political relationship[2]	A and B are allies	Interchange (food for support)	No
David's score difference	B is "stronger"[3]	Sharing under pressure / harassment	Yes
Relatedness	A and B are maternal relatives[4]	Kin selection	Chimpanzees yes, bonobos no
Sex combination	B is from the same / opposite sex	Interchange (♂-♀: food for sex, ♂-♂/♀-♀: food for support); sharing under pressure (chimpanzees: ♀-♂, bonobos: ♂-♀)	No

[1]Only chimpanzees
[2]Only bonobos
[3]i.e. on average more likely to win dyadic conflicts with A
[4]i.e. mother-daughter and mother-son pairs, with most transfers going from mothers to (adult) offspring. The maternal brother pair among the bonobos never shared food. We did not include paternal relatives since there was no evidence that individuals preferentially associated, groomed, supported or shared food with paternal kin (unpublished analyses)
[5]See Table 2-5 for effect sizes (parameter estimates)

Independent variables. We tested the influence of several explanatory variables on food sharing (Table 2-3). *(Tolerated) transfers received[1]*: The proportion of approaches of the current owner to the current approacher that led to (tolerated) transfer when the latter was food owner. *Relationship quality*: Numerical. Following Fraser et al. (2008) we performed a principal components analysis (PCA) on the variables *grooming given* (proportion of scans approacher groomed owner), *support given* (agonistic support given by approacher to owner as proportion of all support given to others) and *proximity* (proportion of scans approacher and owner rested within arm's reach, excluding grooming). A minimum eigenvalue of 1.0 was used to determine the number of components extracted from the PCA (Tabachnik and Fidell 2007). For the chimpanzees, we thus extracted one component, explaining 50.4% of the variance. It had a high positive load of grooming, support and proximity and is thus largely

equivalent to Fraser et al. (2008)'s "*relationship value*" component. For the bonobos, two components were extracted, explaining 45.2% and 34.4% respectively. The first component had a high loading of grooming and proximity but negative loading of support, whereas the second one had a high loading of support, minor loading of proximity and negative loading of grooming. Thus we called the first component "*affiliative relationship*" and the second one "*political relationship*". *David's score difference*: Numerical factor indicating the relative ability of two individuals to win dyadic conflicts, calculated as normalized David's score (de Vries et al. 2006) of the owner minus normalized David's score of the approacher, i.e. the factor is positive for dominant food owners and negative for subordinate ones. We initially included formal ranks of owners and formal rank differences as factors, but found high collinearity in these factors and thus had to consider them redundant. *Relatedness*: Binary factor indicating whether owner and approacher are maternal relatives. *Sex combination*: Factor with 4 levels, female-female, male-male, female-male, male-female.

　　　　Dominance style and reciprocity. Dominance hierarchies were calculated with MatMan 1.1 (de Vries et al. 1993; de Vries 1995) on the basis of pant-grunts for the chimpanzees (Noë et al. 1980) and fleeing upon aggression in dyadic conflicts for the bonobos (Vervaecke et al. 2000). The steepness of dominance hierarchies was calculated as the slope of a linear regression line through the ranked normalized David's scores, based on the outcome of dyadic agonistic interactions (de Vries et al. 2006). While a shallow slope represents an egalitarian dominance hierarchy in which rank differences are small, a steep slope represents a despotic hierarchy with large rank differences (van Schaik 1989; de Vries et al. 2006; Stevens et al. 2007b). Following Stevens et al. (2005) we included only individuals over seven years of age, when they

become socially and sexually mature, and in captivity have been shown to reproduce (chimpanzees: Carlsen (2007); bonobos: Pereboom & Stevens (2008)).

Grooming reciprocity was calculated using rowwise matrix correlations in MatMan1.1. (de Vries 1993; de Vries et al. 1993). The units of analysis were grooming bouts given and received. To compare mean hierarchy steepness and mean grooming reciprocity between the species we first calculated a mean for the repeatedly sampled groups (see Table 2-2) before calculating the mean among independent groups. To analyze the influence of hierarchy steepness on grooming reciprocity we used linear mixed effects models (Pinheiro and Bates 2000), fitted with nlme (Pinheiro et al. 2008) in R 2.9.0 (2009). Since we were interested in the general influence of dominance structure on reciprocity, *hierarchy steepness*, ranging from 0-1, was set as the only explanatory variable. *Species* (binary: chimpanzees/bonobos) and *group identity* were set as random factors. Other factors potentially influencing hierarchy steepness and reciprocity, namely *total group size* (numerical) and *sex ratio* (the proportion of males) were also included as random factors.

Results

General patterns of food sharing

In total we recorded 228 transfers among the chimpanzees and 73 transfers among the bonobos. Chimpanzees were on average food owner during 42.4min (± 43.5) whereas bonobos were food owner during 124min (± 78.3). Thus, chimpanzees on average transferred food almost ten times more frequently than bonobos (21.4 vs. 2.6 transfers per hour of being food owner, $t_{14}=3.02$, $P<0.01$).

Food acquisition. In both species, food owners never approached non-owners and never initiated food transfers, except for one instance among the chimpanzees (Table 2-4). Food was virtually only shared if non-owners approached food owners and actively tried to acquire food by begging or by taking. Peering at a food owner without begging or taking never led to transfer.

Donor - recipient combinations. Among the chimpanzees, 67.2% of all transfers were from dominants to subordinates and 32.8% from subordinates to dominants. Furthermore, 90.4% were among non-kin and 9.6% among kin. Finally, 45.5% of all transfers were from males to females, 27% were among females, 16.9% from females to males, and 10.7% among males. Among the bonobos, 61.2% of all transfers were from subordinates to dominants and 38.2% from dominants to subordinates; 84.3% were among non-kin and 15.7% among kin; 41% of all transfers were among females, 41% from males to females, 16.7% from females to males and 1.2% among males. Whether dominance, kinship or specific sex combinations had an influence on success rates was evaluated in the models below.

Reactions to food approaches. In both species reactions to approaches were mostly negative (chimpanzees: mean ±SD 49.5 ±31.5%; bonobos: 53.4 ±24.1%) or passive (47.9 ±29.9%; 45.9 ±24.6%). Positive reactions were rare (2.6 ±4.7%; 0.7 ±1.2%). In both species, low-ranking food owners showed significantly more negative reactions (Spearman correlation of negative reactions with rank: *Chimpanzees*: rho=0.62, N=10, P=0.05; *Bonobos*: rho=0.83, N=6, P<0.05).

Food-getting success. Average food-getting success (±SD) was significantly higher for chimpanzees (33 ±9%) than for bonobos (19 ±11%, t_{15}=2.97, P=0.01).

Socio-sexual behavior. Bonobo approachers presented sexually to the food owner 23 times (3.5% of approaches) which led to sexual interactions 12 times (1.9% of approaches). In two cases, food was transferred after sexual intercourse. Hence food getting success was not significantly different with or without sexual interactions (16.7% vs. 19%; X^2=0.01, df=1, P=0.9). Chimpanzees never used socio-sexual behavior in food acquisition.

Types of transfers. Contrary to bonobos, chimpanzees fairly often transferred food actively to approachers (Table 2-4). Active forms of transfers (active sharing and facilitated taking) were thus significantly more common among chimpanzees (mean ±SD=13.1 ±13.7% vs. 0 ±0%; t_{14}=2.3, P<0.05). Overall tolerated transfers were also significantly more common among chimpanzees (mean ±SD=71.8 ±32.7% vs. 36.4 ±26.3%, t_{14}= 2.33, P<0.05, Figure 2-1).

Table 2-4: Types of food transfers and their occurrence among chimpanzees and bonobos

	Definition	Chimpanzees	Bonobos
N		228	73
Offering[1]	O[3] initiates transfer without request by A[4]	0.9%	0%
Active sharing[1]	O actively transfers food to A	5.7%	0%
Facilitated taking[1]	O makes movements conducive to transfer but A takes the food	18%	0%
Relaxed claim[1]	O allows A to take food	61.4%	39.7%
Forced claim[2]	A takes food despite resistance by O	13.2%	57.5%
Stealing[2]	A snatches food by surprise, preventing resistance by O	0.9%	2.7%

[1]tolerated transfers
[2]non-tolerated transfers
[3]O=Owner
[4]A=Approacher

In sum, both species rarely responded positively to approachers and low-ranking food owners were more likely to respond negatively. Among chimpanzees most transfers were from dominants to subordinates while the opposite was true for the bonobos. Chimpanzee food owners allowed higher food-getting success and more

tolerated taking and also transferred food more actively than bonobos. The latter only rarely engaged in sexual interactions during sharing without any effect on success.
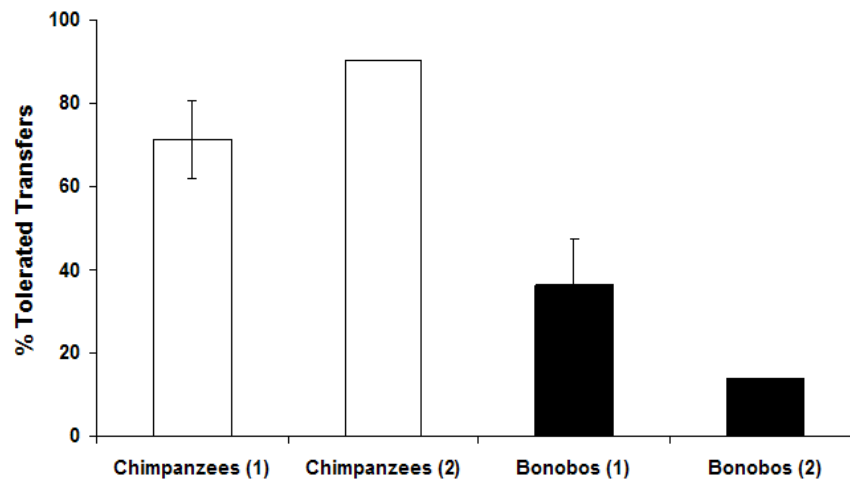
Figure 2-1: The average percentage (±SEM) of tolerated food transfers for chimpanzees and bonobos as observed in this study and by de Waal (1992). In both studies, chimpanzees shared food more tolerantly than bonobos

Mechanisms of food sharing

Chimpanzees. For tolerated transfers given, the full model explained significantly more variance in the data than the null model (LR=37.16, df=7, P<0.001). The parameter estimates of the most parsimonious model are given in Table 2-5. Relatedness explained most of the variance in that model (LR=5.42, df=1, P<0.05), followed by tolerated transfers received (LR=3.78, df=1, P<0.05) and, to a lesser extent, David's score difference (LR=8.36, df=1, P=0.09) and relationship value (LR=1.39, df=1, P=0.26), the former of which had a negative influence. This indicates that reciprocity explained most of the food transfers among non-kin. While closely affiliated

dyads also shared more, dominant food owners were less likely to tolerate food taking than subordinate ones.

For all transfers given, the full model also explained significantly more variance than the null model (LR=25.95, df=7, P<0.01). The parameter estimates of the most parsimonious model are given in Table 2-5. Transfers received (LR=10.29, df=1, P<0.001) and relatedness (LR=8.31, df=1, P<0.01) best explained transfers given. This indicates that reciprocity and kin benefits best explain overall food transfers.

Table 2-5: The parameter estimates for the most parsimonious GLMM explaining (tolerated) food transfers given by chimpanzees and bonobos. For both measurements of food sharing there is a reciprocal relationship among the chimpanzees but not the bonobos. ^{NS} P>0.1, ° P<0.1, * P<0.05, ** P<0.01, ***P<0.001

Food sharing measure	Chimpanzees		Bonobos	
	Factor	β ±SE[1]	Factor	β ±SE[1]
Tolerated transfers given	*Intercept*	-2.23 ±0.28***	*Intercept*	-3.49 ±0.52***
	Tolerated transfers received	1.53 ±0.78*	*Affiliative relationship*	0.71 ±0.28*
	Relationship value	0.16 ±0.13^{NS}		
	Relatedness	1.49 ±0.63*	*David's score difference*	-0.37 ±0.27 ^{NS}
	David's score difference	-0.51 ±0.15**		
All transfers given	*Intercept*	-1.89 ±0.31***	*Intercept*	-1.41 ±0.43***
	Transfers received	1.53 ±0.47**	*Transfers received*	-3.14 ±1**
	Relatedness	1.48 ±0.52**	*Affiliative relationship*	0.8 ±0.24***
			David's score difference	-0.4 ±0.23^{NS}

[1]Coefficients (±SE) of the factors retained in the most parsimonious model based on AICc.

Bonobos. For tolerated transfers given, the full model did not explain significantly more variance than the null model (LR=14.75, df=8, P=0.34). The most parsimonious model (Table 2-5) only approached significance (LR=10.9, df=2, P=0.08) and included affiliative relationship (LR=4.57, df=1, P=0.23) and, with negative

influence, David's score difference as factors (LR=1.76, df=1, P=0.19), none of which explained a significant amount of the variance. This indicates that bonobos tolerated transfers more by closely affiliated approachers but less by subordinate ones .

For all transfers given, the full model explained significantly more variance than the null model (LR=30.47, df=8, P<0.01). Transfers received when not an owner was a significant factor in the full model ($\beta \pm SE=-4.04 \pm 1.09$, P<0.001) and had a significant but *negative* influence on transfers given (LR=15.1, df=1, P<0.01). In the most parsimonious model (see Table 2-5), transfers given was strongly negatively influenced by transfers received (LR=11.55, df=1, P<0.01) and mildly positively influenced by affiliative relationship (LR=9.63, df=1, P=0.09). David's score difference shows the main direction of transfers, to individuals likely to win conflicts, but did not explain a significant amount of the variance (LR=3.18, df=1, P=0.19). This indicates that food transfers among bonobos were unidirectional, from subordinates to dominants especially if they were closely affiliated.

In sum, both measurements of food transfers given were significantly explained by food transfers received for the chimpanzees, thus indicating reciprocal exchange (Figure 2-2). Relatedness and relationship value also had positive influences on food transfers given. The fact that relationship value was only an important factor for tolerated transfers but not all transfers shows that owners may share with preferred individuals if they have a choice, which was restricted when transfers were forced. No model could significantly explain tolerated transfers given by bonobos, although affiliative relationship tended to influence it. Transfers received had a significant and *negative* effect on transfers among the bonobos, thus strongly indicating that transfers

were mainly unidirectional. Hence food sharing seemed to be reciprocal among chimpanzees but not among bonobos.

a)   b)
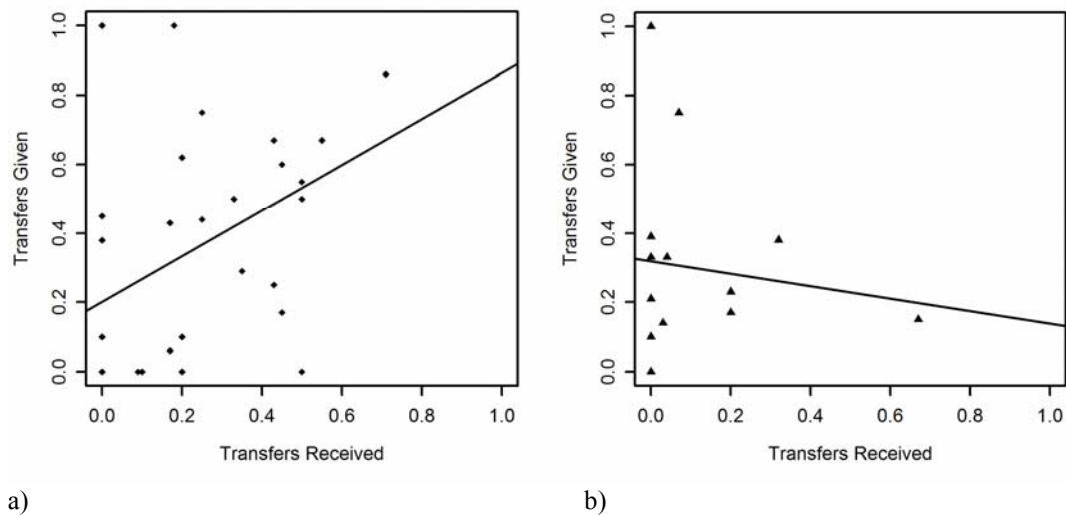
Figure 2-2: The relation between food transfers received (as the proportion of successful approaches) and food transfers given for a) chimpanzees (squares) and b) bonobos (triangles). There was a significant positive influence of food received on food given among the chimpanzees, indicating reciprocity, but a significant negative one among the bonobos, indicating mainly unidirectional transfers

Dominance and reciprocity

The chimpanzees in this study had a shallower and less linear dominance hierarchy than the bonobos (slope: chimpanzees 0.18; bonobos 0.54, linearity: 0.44; 0.6) and can thus be called more egalitarian. Across all sampled groups, chimpanzees had shallower hierarchy steepness (3 independent groups; mean $\pm$SD = 0.16 $\pm$0.02) than bonobos (4 independent groups; 0.73 $\pm$0.07; t_5=14.12, P<0.001) and higher grooming reciprocity coefficients (0.82 $\pm$0.1 vs. 0.29 $\pm$0.26; t_5=3.3, P<0.05). In a linear mixed effects model including species and group identity as random factors, hierarchy

steepness had a significant negative influence on grooming reciprocity (AICc=12.16, β±SE=-0.81±0.19, t_5=-4.24, P<0.01, Figure 2-3). Even after including group size and sex ratio as additional random factors, hierarchy steepness still tended to negatively influence grooming reciprocity (AICc=41.46, β±SE=-0.64±0.26, t_3=-2.42, P=0.09), but the AICc of this model was significantly higher, indicating that these factors did not help explain more variance in the data.
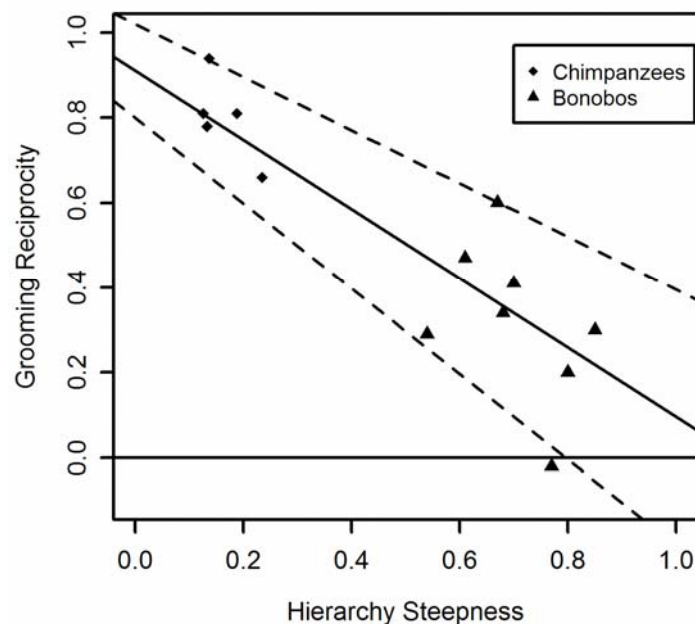
Figure 2-3: The influence of hierarchy steepness on grooming reciprocity among different groups of chimpanzees (squares) and bonobos (triangles). The full line is the predicted curve fitted with a linear mixed effect model, controlling for species and repeated measures of the same groups. The dotted lines represent the standard errors of the fitted curve. Hierarchy steepness had a significant negative influence on grooming reciprocity (P<0.01)

Discussion

We hypothesized that both the ultimate and the proximate mechanisms for sharing food are influenced by the dominance structure of a group. In this study, individuals of neither species tended to encourage food transfers but most often ignored approaches or made movements impeding food transfer, especially if low-ranking. This indicates that low rankers had to avoid forced transfers more than high rankers, i.e. did not enjoy a "respect for possession" (Kummer and Cords 1991). Chimpanzees were significantly more successful in acquiring food from others than bonobos. Sexual interactions were only rarely observed among bonobos and did not alter food-getting success. Chimpanzees also shared food more actively and tolerantly while bonobos often forced transfers. Thus, chimpanzees were more prosocial (Table 2-4).

We predicted that reciprocal exchange was more likely if transfers are tolerated rather than forced. Among chimpanzees, forced transfers were rare and the results of both models strongly indicate that food transfers were reciprocated. Among bonobos, forced transfers were common and the overall model indicated that food transfers were unidirectional. If only tolerated transfers were considered, bonobos tended to share more with closely affiliated individuals, however, this model could not explain a significant amount of the variance in the data. Thus, chimpanzees reciprocated food transfers but bonobos did not (Figure 2-2). General relationship components included in the model never explained a significant amount of the variance, suggesting that food was, if at all, traded for itself rather than for grooming, support or shared proximity. Similarly, Gurven et al. (2000) found that meat received was the best predictor for meat given. However, other studies did find reciprocal exchange of food with other currencies (cf. Nishida et al. 1992; Mitani 2006; Gomes and Boesch 2009) and we also

found some interchange with grooming and support among the chimpanzees using matrix correlations (unpubl. analyses), hence these differences may partly be due to the choice of statistical method.

From our results, we cannot make inferences about the proximate regulations of reciprocal exchange. The observed patterns are consistent with symmetry-based, attitudinal- or calculated reciprocity (Brosnan and de Waal 2002). However, it is most parsimonious to assume symmetry-based reciprocity, especially since analyses on short-term contingency of exchange (i.e. within hours, cf. de Waal 1997) were not significant in our study groups (Jaeggi et al. in prep.). Thus, over the whole study period, food exchanges were on average reciprocal within dyads, but giving was not necessarily contingent on receiving, since the latter may have happened before or after the former.

We found differences in dominance style that were consistent with the observed patterns of food sharing and reciprocity. The chimpanzee group was more egalitarian and was thus expected to share more tolerantly and more reciprocally. The bonobos were more despotic, which can explain why transfers were mainly forced and unidirectional, from subordinates to dominants. In a comparison of several groups of chimpanzees and bonobos, the latter were more despotic and hierarchy steepness was a significant negative predictor of reciprocity in grooming (Figure 2-3), thus confirming the pattern found in food sharing. A model including other factors potentially influencing both grooming reciprocity and hierarchy steepness, namely total group size and sex ratio, explained less variance in the data. Thus hierarchy steepness seems to be a robust predictor of reciprocity in grooming across different populations of chimpanzees and bonobos; whether this effect also holds for patterns in food sharing remains to be tested.

While the food type most commonly shared among wild chimpanzees and hunter-gatherers is meat (Table 2-1; Gurven 2004), we used plant food (fruits or vegetables). Could this affect sharing patterns? Moore (1984) noted two characteristics of meat which make it prone to sharing: First, meat is easily carried and shielded and thus highly defendable. The same is true for the large fruits commonly shared by wild bonobos (*Treculia africana* and *Anonidium mannii*: White 1994; Fruth & Hohmann 2002) and chimpanzees (Cultivated fruits: Hockings et al. 2007), the bundles of browse used by de Waal (1989; 1992; 1997) and the paper bags used in this study (as long as they were not torn, which happened only rarely). Second, meat is only infrequently available and of high quality, making it highly attractive. While this is again true to some extent for the large fruits cited above, it applies less to the food sources in this study since they consisted of parts of the apes' daily diet. However, in both groups the individuals were always highly motivated to acquire food, despite the relatively low attractiveness. Furthermore, de Waal (1989; 1997) already showed that reciprocal sharing patterns may emerge from relatively low-quality food. Finally, bonobos in the wild also regularly hunt and share meat (Hohmann and Fruth 1993; Fruth and Hohmann 2002; Hohmann and Fruth 2008; Surbeck and Hohmann 2008) with a frequency that may well have been underestimated in the past (Stanford 1998). Hence, even though meat may be shared more actively than large fruits within the same population (D. Watts, pers.comm.), there is no a priori reason to relate interspecies differences in sharing patterns or -psychology to resource type.

It is noteworthy, that the three studies directly comparing chimpanzees and bonobos in similar competition situation, namely monopolizable food sources, did find conflicting results concerning tolerance (de Waal 1992; Hare et al. 2007; this study).

However, this could be due to the fact that tolerance was measured differently: Whereas Hare et al. (2007) measured the tendency to *monopolize* food, de Waal (1992) and our study measured the tendency to *share* food (once monopolized). Given this difference, direct comparison between these studies is difficult. However, a greater tendency both to monopolize *and* to share in chimpanzees would be consistent with evolutionary models emphasizing both the benefits of being food owner per se and of selective sharing (e.g. Moore 1984). In fact, if sharing has direct benefits, individuals are expected to seize every possible opportunity for sharing. This is consistent with the commonly observed scramble for ownership after hunts, followed by relatively peaceful sharing (e.g. Nishida et al. 1979; Nishida et al. 1992). Hence the two tendencies might even be psychologically linked.

Our inter-specific analysis of hierarchy steepness and grooming reciprocity (Figure 2-3), along with intra-specific correlations (Stevens et al. 2005; Schino and Aureli 2008), suggests that hierarchy steepness could be a valuable predictor of reciprocity expected in other species or at least other populations of chimpanzees and bonobos. The fact that Schino and Aureli (2008) did not find an effect across species may be because their data set lacked relatively egalitarian species for comparison. This relation could easily be tested with data from other populations of chimpanzees and bonobos.

Some studies on food sharing in chimpanzees or bonobos report reciprocal exchange (de Waal 1989; de Waal 1997; Mitani and Watts 2001; Mitani 2006) while others found more support for sharing-under-pressure (Fruth and Hohmann 2002; Gilby 2006). In our study, reciprocal exchange was found among the chimpanzees but not among the bonobos, where sharing-under-pressure better explained food transfers. As

Stevens and Gilby (2004) and Gilby (2006) have pointed out, the two hypotheses are not mutually exclusive. Rather, there may be a behavioral continuum between the possibility for reciprocal exchange, when the costs of defending food are low and owners can selectively share with particular individuals, and sharing-under-pressure, when the costs of defending food are high and transfers are mainly from subordinates to dominants (see also Moore 1984). The steepness of the dominance hierarchy may determine the position of groups on this continuum and could thus be helpful in predicting the patterns of food sharing in different populations.

Similarly, at the proximate level, food transfers among chimpanzees and bonobos can range from highly tolerant and active to reluctant or forced (Teleki 1973; Kuroda 1984; Boesch and Boesch 1989; Nishida et al. 1992; Fruth and Hohmann 2002; Gilby 2006; Surbeck and Hohmann 2008). The amount of active sharing (active giving and facilitated taking) among the chimpanzees in this study was relatively high compared to other populations (this study: ~24%; Taï: ~7% (Boesch & Boesch 1989); Gombe: 1.2% (Teleki 1973); Yerkes: 0.5% (de Waal 1989)), suggesting higher degrees of prosociality. However, these differences could also be due to different food types and group compositions. Among wild bonobos, food sharing seems to be largely tolerant (Kuroda 1984; White 1994; Fruth and Hohmann 2002), but in captivity, food transfers were found to be more tolerant among chimpanzees than among bonobos (de Waal 1992; this study). While general discrepancies between captivity and the wild, e.g. the lack of fission-fusion dynamics might explain some of these differences, our results suggest that they may also be related to the steepness of the dominance hierarchy in a given population (within a captivity or wild context). Pending formal attempts to explain differences in reciprocity or tolerance in food sharing within or between species

(Mitani 2009), more data on hierarchy steepness from other populations of chimpanzees and bonobos could provide a valuable test of our hypothesis.

The fact that in this study bonobos were less tolerant and more despotic than chimpanzees may seem unexpected, given that although chimpanzees can be characterized as relatively egalitarian (Boehm 1999) bonobos have often been described as more tolerant and egalitarian (de Waal and Lanting 1997; Hare et al. 2007). However, this strict dichotomy has recently been questioned. First, Stanford (1998) suggested that reported behavioral differences may be due to the relative paucity of data on wild bonobos and the different research focus in the two species. Second, comparisons of various wild populations indicated that levels of sociality, which depend on food availability and the resulting feeding competition, may lie on a continuum for the two species rather than representing a dichotomy (Hohmann and Fruth 2002; Stumpf 2007). Finally, various captive groups of bonobos were shown to exhibit high rates of (serious) aggression and consistently steep hierarchies, resulting in 'semi-despotic' societies (Stevens et al. 2008), which may be a response to increased contest competition under captive conditions (cf. Gore 1993). In general, it is difficult to maintain clear species differences as expressed levels of sociality, dominance relationships, aggression and playfulness in *both* species may well lie on a continuum dictated by the levels of feeding competition (van Schaik 1989; Stanford 1998; Stumpf 2007) and space availability (Aureli and de Waal 1997; Sannen et al. 2004; Tacconi and Palagi 2009).

Human foragers are characterized as relatively egalitarian (Woodburn 1982) and group-wide sharing of meat is universal, largely voluntary and often reciprocal (Gurven 2004). In fact, all studies statistically testing reciprocal exchange found significant

evidence for it (Gurven 2004) and in a multivariate analysis similar to ours, Gurven et al. (2000) also found that food received was the best predictor of food given. Our results indicate that a relatively egalitarian hierarchy may have favored such reciprocal exchange due to increased control of owners over food distribution. During evolutionary (and ontogenetic) history, food owners should become more tolerant to requests by those likely to reciprocate. They may also start to share more actively, which could reflect genuine altruistic dispositions and thus induce greater feelings of gratitude in the recipient, resulting in even better reciprocation (Trivers 1971).

In sum, we suggested that a shallow dominance hierarchy allows food owners to selectively tolerate requests by those individuals who reciprocate. We found that chimpanzees were more egalitarian than bonobos and shared more tolerantly and reciprocally. A cross-species analysis of the influence of despotism on grooming reciprocity confirmed this pattern. We conclude that a relatively shallow dominance hierarchy was an important precondition for the evolution of extensive food sharing in humans and the prosocial predispositions related to it.

Chapter 3: Mechanisms of reciprocity in food sharing among chimpanzees and bonobos: Short-term contingency and the grooming effect

Reciprocity can ultimately explain many instances of altruistic behavior among animals, yet its proximate regulation remains poorly understood. While there is ample evidence for a long-term statistical contingency between services given and received among non-human primates, evidence for a short-term behavioral contingency has been controversial. Here we tested for such short-term contingencies using data on food sharing, grooming and agonistic interactions in captive chimpanzees and bonobos. The only effect we found was that bonobos were more likely to be allowed to take food if they had groomed the food owner previously, regardless of whether they did so more or less than usual. We conclude that grooming selectively increased the food owners' tolerance. This cognitively simple proximate mechanism may lead to contingent exchange, given the chance for reciprocation after grooming, and may explain some of the other results on short-term contingencies. No effect was found among the chimpanzees, probably because sharing tolerance was already at ceiling level due to higher levels of long-term tolerance. Furthermore, no evidence for punishment or retaliation was found as sharing generosity and aggression were not associated in any way and no evidence for indirect reciprocity as third parties did not groom generous individuals more. We conclude that long-term reciprocity is more important among chimpanzees and bonobos while calculative, tit-for-tat like exchanges only became

prominent in humans with the advent of trade and the resulting interactions between relative strangers.

Introduction

Reciprocal altruism (henceforth: *reciprocity*) has been a major evolutionary explanation for many instances of human and animal cooperation (Trivers 1971; Trivers 2006). Reciprocity requires a contingent behavioral strategy, namely that actors direct altruistic acts selectively to those that have directed altruistic acts to them in the past or are likely to do so in the future, thus profiting both partners. Many animal species, and in particular non-human primates have been shown to exhibit reciprocal patterns of exchange in various measured currencies such as food sharing, grooming and agonistic support (reviews and meta-analyses by Schino 2007; Schino and Aureli 2008; Schino and Aureli 2009; Jaeggi and van Schaik in review). However, while most evidence for reciprocity was based on a *statistical contingency* of services given and services received, it is disputed whether this reflects a *behavioral contingency* (Stevens and Hauser 2004; Clutton-Brock 2009). Hence, the proximate regulation of reciprocal exchange among animals remains less well understood (Brosnan and de Waal 2002; Schino and Aureli 2009).

These differences between statistical and behavioral contingency of reciprocation have been formalized in terms of three different types of proximate regulations of reciprocity (Brosnan and de Waal 2002, p.259): "Symmetry-based reciprocity *is cognitively the least complex form, based on symmetries inherent in dyadic relationships (e.g., mutual association, kinship). Attitudinal reciprocity, which is more cognitively complex, is based on the mirroring of social attitudes between*

partners ... Finally, calculated reciprocity, *the most cognitively advanced form, is based on mental scorekeeping*". Symmetry-based reciprocity thus only requires some consistent pattern of association between specific individuals, leading to statistical reciprocity in the long term, and can probably explain many instances of animal reciprocity. The two other forms require a contingency of exchange over short time-periods (e.g. de Waal 1997; de Waal 2000), the evidence for which is much more controversial (Table 3-1). Note that it is not quite clear whether or how attitudinal and calculated reciprocity lead to different predictions regarding observable contingencies, which is probably why most researchers speak only of calculated reciprocity. We will here use the term *contingent reciprocity* to refer to both types.

Interestingly, the more naturalistic studies in Table 3-1 with higher ecological validity found mainly positive evidence for contingent reciprocity (Seyfarth and Cheney 1984; Hemelrijk 1994; de Waal 1997; Koyama et al. 2006) whereas more artificial experiments with lower ecological validity found little evidence (Melis et al. 2008; Brosnan and Beran 2009; Brosnan et al. 2009; Pele et al. 2009; Yamamoto and Tanaka 2009a; Yamamoto and Tanaka 2010). Thus it seems that the chances of a positive result are higher in naturalistic studies, which may result from a lack of direct interactions in more artificial experiments (Yamamoto and Tanaka 2010, see Discussion). On the other hand, while the underlying cognitive mechanisms are difficult to infer from naturalistic observations (e.g. Hemelrijk 1994), at least without invoking a great deal of anthropomorphic assumptions (e.g. Koyama et al. 2008; see Wright 2006; Barrett et al. 2007 for simpler explanations), those artificial experiments that did find positive results may more safely infer cognitively advanced processes such as mental scorekeeping (Dufour et al. 2009).

Furthermore, it is noteworthy that the optimal type of reciprocity depends on the social partner. Both humans and non-human primates tend to form stable social relationships (friendships) within which services are exchanged reciprocally on a long-term basis (Trivers 1971; Silk 2002). The affiliative emotions and trust that prevail in friendships buffer them against short-term fluctuations in cooperative tendencies or abilities of the partners, the probability of cheating is low and there is now need to constantly track the exchange of services. Thus, friendships are associated with symmetry-based reciprocity. On the other hand, socially distant partners may rely more on contingent reciprocity, because the probability of cheating is higher. Thus, exchange in socially distant relationships is less buffered by trust and recent interactions may weigh more heavily. Some evidence for such a stronger effect of recent interactions in more distant partners has been found by de Waal (1997).

Reciprocity can not only be positive, through the exchange of services, but also negative, through the punishment of cheaters by "moralistic aggression" or "retalitation", i.e. the withholding of future benefits (Trivers 1971; Clutton-Brock and Parker 1995; Stevens and Hauser 2004). Initially, de Waal (1989, p. 456) reported evidence for punishment and proposed that "*aggression appears to be a functional aspect of the reciprocity system* [of chimpanzees]". However, his evidence was based on a negative correlation of food sharing generosity and aggressive rejections received when requesting food *on other occasions* by *any other group member*, averaged across a three month study period. Such a long-term correlation could also be due to hidden factors such as rank, which may influence both variables. In fact, the most generous individual in de Waal's group was also the most dominant (the only male), and thus never received aggression. If he is removed the correlation becomes non-significant. On

the other hand, if punishment is triggered by indignation (Trivers 1971), it should occur, or at least be strongest immediately after a cheating event (such as a failure to share food) and should mainly be performed by those cheated upon (in contrast to "altruistic" punishment, which is performed by third parties but thus suffers from second order free-riding problems and among humans is only common in large-scale societies (Marlowe et al. 2008). Hence altruistic punishment is not expected in animals). Such forms of punishment have been reported by Hauser and Marler (1993). Other solid evidence for punishment among non-human primates however remained scarce (reviewed by Stevens and Hauser 2004; Jensen in press).

Finally, among humans, both positive reciprocity, i.e. the rewarding of cooperators, and negative reciprocity, i.e. the punishment of cheaters, can involve third parties. Thus, generalized or *indirect reciprocity* refers to the rewarding of cooperators by third parties (Trivers 1971; Alexander 1987) and *altruistic punishment* refers to the punishment of cheaters by third parties (Fehr and Gachter 2002). Many scholars have suggested that such third party mechanisms are a relatively recent feature of human cooperation, arising only with large-scale societies (Trivers 1971; Marlowe et al. 2008; Roberts 2008; Henrich et al. 2010), and accordingly no evidence has been found so far in non-human primates.

Thus, in order to contribute to the debate about the proximate mechanisms underlying reciprocity in animals we used data resulting from naturalistic food sharing experiments in one captive group of bonobos and chimpanzees respectively to test for short-term contingencies and punishment. This study is important since it includes a previously untested species (Bonobos, see Table 3-1) and is of high ecological validity. Food sharing has been one of the main contexts in which questions regarding

reciprocity have been investigated, both among non-human and human primates (reviewed by Brown et al. 2004; Gurven 2004). The study was designed after previous naturalistic food sharing studies with positive results (de Waal 1989; de Waal 1997) such that negative results in our study could not be explained by experimental design.

Previous results from the same subjects showed that food sharing was reciprocal on a long-term basis among the chimpanzees but not the bonobos, and that exchanges for other services such as grooming and agonistic support at least partly explained sharing in both species (Jaeggi et al. 2010b). Furthermore, both grooming and agonistic support were reciprocal in the long-term among the chimpanzees but not the bonobos. Hence, we expected short-term effects to be more pronounced among the bonobos and less so among the chimpanzees since the latter seemed to rely more on symmetry-based reciprocity.

Since no evidence for indirect reciprocity had been reported for non-human primates, we did not expect to find any in our study groups.

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Table 3-1: Studies testing for contingent reciprocity among primates. All studies included some element of temporal contingency between services given and services received

Species	Ecological validity[a]	Exchange type	Contingent Reciprocity?	Reference	Author's conclusion
Chimpanzees *Pan troglodytes*	High	Sharing food after being groomed	Yes, but small effect size, larger for socially distant dyads	(de Waal 1997)	"we at present have evidence for the entire set of features expected if reciprocity were cognition-based: partner-specificity, selective protest, retaliation, turn-taking, and the effect of one service on another." (p. 384)
	High	Agonistic support after grooming, aggression after support/no support	Yes, but only for aggressor (not victim) support	(Koyama et al. 2006)	"We found evidence of a system of reward and punishment. … The findings are consistent with a mechanism of calculated interchange in chimpanzees." (p. 1293)
	Moderate	Experiment 1: Cooperate with recruiter	Weak effect	(Melis et al. 2008)	"models of immediate reciprocation and detailed accounts of recent exchanges (e. g. Tit for Tat) may not play a large role in guiding the social decisions of chimpanzees" (p. 951)
	Low	Experiment 2: Turn-taking in targeted helping	Weak effect	(Melis et al. 2008)	
	Low	Turn-taking in food delivery experiment	With difficulty, not spontaneously	(Yamamoto and Tanaka 2009a)	"These findings suggest that there is some difficulty in the occurrence of reciprocal cooperation in chimpanzees. Chimpanzees, differently from humans, might play a donor's role only on the partner's request, but not spontaneously." (p. 242)
	Low	Turn-taking in food delivery experiment	No	(Brosnan et al. 2009)	"We conclude that contingent reciprocity does not spontaneously arise in experimental settings, despite the fact that patterns of behavior in the wild indicate that individuals cooperate preferentially with reciprocating partners." (p. 587)
	Low	Bartering with tokens	Only after extensive training and via experimenter	(Brosnan and Beran 2009)	"It appears that extensive barter may represent a relatively recent evolutionary development in the hominid lineage." (p. 193)
	Low	Token exchange	No	(Pele et al. 2009)	"The analyses showed no evidence for calculated reciprocity in interactions" (p.375)
	Low	Turn-taking in food delivery experiment	No	(Yamamoto and Tanaka 2010)	"We propose that the experimental set-up which prevented direct interactions between the participants might have influenced these results. In conclusion, the present study suggests that voluntary and/or strategic other-rewarding behaviour arose in humans after divergence from the common ancestor of humans and chimpanzees." (p. 595)

Species					
	High	Sharing after grooming/aggression, aggression/grooming after sharing	No (see results)	this study	see discussion
Bonobos *Pan paniscus*	Low	Token exchange	No	(Pele et al. 2009)	"The analyses showed no evidence for calculated reciprocity in interactions" (p.375)
	High	Sharing after grooming/aggression, aggression/grooming after sharing	Some (see results)	this study	see discussion
Gorillas *Gorilla gorilla*	Low	Token exchange	No	(Pele et al. 2009)	"The analyses showed no evidence for calculated reciprocity in interactions" (p.375)
Orangutans *Pongo abelii*	Low	Token exchange	Yes	(Dufour et al. 2009)	"This study is the first experimental demonstration of the occurrence of direct transfers of goods based on calculated reciprocity in non-human-primates" (p. 172)
	Low	Token exchange	No	(Pele et al. 2009)	"The analyses showed no evidence for calculated reciprocity in interactions" (p.375) "Only once did we observe an episode … between a pair of orangutans that might have represented an instance of calculated reciprocity" (p. 381)
Long-tailed macaques *Macaca fascicularis*	High	Agonistic support after being groomed	Yes, but only for aggressor (not victim) support	(Hemelrijk 1994)	"From a cognitive point of view, one would be inclined to assume that individuals who exchange acts must remember the identity of the groomer. This, however, is not proven by these experiment nor by those of Seyfarth & Cheney" (p. 481)
Vervet monkeys *Cercopithecus aethiops*	High	Agonistic support after being groomed	Yes, but only for aggressor (not victim) support (not actual support but response to play-back measured)	(Seyfarth and Cheney 1984)	"Vervets appear to be more willing to aid unrelated individuals if those individuals have behaved affinitively toward them in the recent past" (p. 541)
Capuchin monkeys *Cebus apella*	Moderate	Turn-taking in food sharing paradigm	Yes	(de Waal 2000)	"Instead of a symmetry-based reciprocity explanation, a mediating role of memory is suggested, and a mirroring of social attitude between partners." (p. 253)

	Moderate	Sharing with cooperation partner	Yes	(de Waal and Berger 2000)	"The increase in sharing following cooperation may rest on psychological mechanisms as complex as mental score-keeping of services and "gratitude", or as simple as attitudinal reciprocity." (p. 563)
Cotton-top tamarins *Saguinus oedipus*	Low	Turn-taking in food delivery experiment	Yes	(Hauser et al. 2003)	"[Tamarins] give more food to those who give food back. Tamarins therefore have the psychological capacity for reciprocally mediated altruism." (p. 2363)

[a]How naturalistic is the study? High ecological validity refers to naturalistic observations of a whole social group where nothing (Seyfarth & Cheney 1984; Koyama et al. 2007) or only a few factors were manipulated (e.g. monopolizable food provided: de Waal 1997; this study; grooming and aggression induced: Hemelrijk 1994). On the other hand, low ecological validity refers to highly artificial experimental set-ups (e.g. subjects spatially separated from recipient and rest of group, food delivery via apparatus rather than through direct interaction: Hauser et al. 2003, Brosnan et al. 2009, Dufour et al. 2009, Yamamoto & Tanaka 2009, 2010)

Materials and methods

The subjects, housing, experimental procedures, food sharing definitions, observation methods and observation hours were the same as described in Jaeggi et al. (2010, main study groups). The number of experimental food sharing sessions was n=30 for the chimpanzee group and n=53 for the bonobo group during which n=758 and n=659 approaches to food owners were recorded respectively.

Variables

In order to test for short-term contingencies, we related the *food-getting success* (FGS), i.e. the proportion of approaches leading to food transfer (de Waal 1989) for a particular owner-approacher dyad in a particular food sharing session to various measures of other services (Table 3-2). FGS was measured twice, once including only tolerated, i.e. un-resisted transfers (excluding forced transfers), and once including all transfers. Note that the difference between the two measures is much larger among the bonobos due to the high proportion of forced transfers (58%, Jaeggi et al. 2010). Differences in the influence of other factors on these two measures of FGS will allow us to infer whether an observed difference in FGS was due to an increased tolerance by the food owner (in which case only the FGS for tolerated transfers should be affected) or due to an increased assertiveness by the approacher (in which case both measures of FGS should be affected). We report detailed values only for FGS based on tolerated transfers unless there are qualitative differences.

To test for positive reciprocity, we related food sharing to grooming. Following de Waal (1997), we scored grooming of the food owner by the approacher previous or

subsequent to the sharing session as a simple binary variable (*grooming yes/no*). This variable may measure whether owners were affected by previously received grooming (e.g. through increased endorphin levels) and whether this would lead to partner-specific tolerance, but not necessarily whether such an effect is due to some kind of score-keeping. To test more specifically for the latter, we also measured whether the approacher groomed the owner *more or less than usual*, by calculating a directional consistency index (DCI: van Hooff and Wensing 1987) of grooming for each owner-approacher dyad:

$$DCI = (a\text{-}o)/(a\text{+}o)$$

where *a* is the number of grooming bouts from approacher to owner and *o* vice versa. Thus, the DCI could range from -1 (owner always groomed approacher) to +1 (approacher always groomed owner). We then calculated the *difference in DCI* within one hour before/after a sharing session compared to the baseline DCI. Thus, this difference in DCI could range from -2 to +2 and measures whether an approacher groomed an owner more or less than usual. Hence, if owners respond to recently built up debt, sharing is expected to occur more for positive values, i.e. when the approacher groomed the owner more than usual. The least sharing is expected at -2 (usually only approacher ever grooms owner *but today only owner groomed approacher*) and the most sharing at +2 (vice versa).

In order to test for negative reciprocity (punishment and retaliation), we tested the effect of previous aggression on FGS and the effect of FGS on subsequent aggression (Table 3-2). Furthermore, aggressive rejections and food-distribution rates were calculated as by de Waal (1989) and averages over the whole study period were correlated (see Appendix 3-1).

To test for the possibility of indirect reciprocity we measured the influence of second parties' FGS on subsequent grooming by third parties, i.e. individuals not previously involved in the sharing interactions. Similar to the second party analyses, we measured grooming received as a binary variable *grooming yes/no* and also the *difference in grooming*. The latter was measured as the difference in grooming duration in seconds after sharing sessions compared to a control period on the next experimental day on which the former food owner was not owner. Note that this analysis could not be done for the bonobos because of the small group size and the consequent lack of third parties.

Statistical analyses

For analyses with specific dyads as the unit of sampling we used generalized linear mixed effects models (GLMM: Bolker et al. 2009), including both the identity of the owner and of the approacher as random factors. For the third party analyses only the identity of the owner was included as a random factor. GLMM's were fitted with lme4 (Bates and Maechler 2010) in R 2.11.0 (R Development Core Team 2010) with binomial error distribution if the response variable was a proportion or binary, and Gaussian error distribution for response variables with normally distributed residuals (only *difference in DCI* and *difference in grooming* by third parties). For models with strong over-dispersion (dispersion parameter >1.2), GLMM's could not be applied because quasibinomial error distributions are as yet not well implemented in GLMM's. Instead, the respective generalized linear model (GLM) was used, with quasibinomial error distribution and the former random factors included as fixed factors. For binomial GLMM's, the amount of variance explained by fixed factors was tested with a

likelihood ratio test against a posterior distribution of likelihood ratios following 1,000 Monte Carlo simulations (Faraway 2006). The parameter estimates β (± Standard errors SE), the likelihood ratio (LR), degrees of freedom (df) of the test and P value are reported. For Gaussian models, we used Markov Chain Monte Carlo sampling with 10,000 iterations in languageR (Baayen 2009) to calculate posterior means of parameter estimates as well as 95% confidence intervals (CI) and P values of these means. For GLM's, the fixed factors were tested with F-tests which are reported together with the parameter estimates. One issue with negative results is the statistical power of the test and the resulting chance of accepting the null hypothesis even though it may be false. To address this we report the statistical power for each test. However, no power analyses are available for GLM(M)'s, hence we report the power of the respective general linear model. For analyses with individual means as unit of sampling we used two-tailed non-parametric tests with exact P values.

Table 3-2: List of the variables, their definitions and whether a statistically significant association with food-getting success (FGS) was found

Variable	Definition	Effect on/of FGS?
Previous grooming	Did the approacher groom the owner within 1h before the session, yes or no	Chimpanzees no, bonobos yes (only voluntary transfers)
Previous difference in DCI	Did the approacher groom the owner *more or less than usually* within 1h before the session	Chimpanzees no, bonobos yes (only voluntary transfers)
Previous aggression	Did the approacher aggress the owner within 1h before the session, yes or no	Chimpanzees no, bonobos yes (all transfers)
Subsequent grooming	Did the approacher groom the owner within 1h after the start of a session, yes or no	No
Subsequent difference in DCI	Did the approacher groom the owner more or less than usually within 1h after the start of a session	No
Subsequent aggression	Did the approacher aggress the owner within 1h after the start of a session	No

Results

Chimpanzees

Positive reciprocity: Among the chimpanzees, food-getting success was not significantly increased by previous grooming by the approacher (mean with grooming (±SEM)= 0.29 (±0.07), mean without grooming= 0.23 (±0.02); GLMM: β ±SE = 0.41 ±0.33; LR=55.05, df=1, P=0.40, Power=0.16) nor by difference in DCI (GLMM: β ±SE = 0.02 ±0.23; LR=53.61, df=1, P=0.38, Power=1.0). In turn, FGS did not significantly affect subsequent grooming by approachers (mean before grooming (±SEM)= 0.29 (±0.09), mean before no grooming= 0.23 (±0.02); GLMM: β ±SE = 0.36 ±0.54; LR=0.42, df=1, P=0.50, Power=0.74), nor deviation from DCI (GLMM: β (95%CI) = 0.08 (-0.11 – 0.14), P=0.90, Power=0.78). Thus, no effects of grooming on food sharing and vice versa were found, even though the power of these models was relatively high.

Furthermore, there was no evidence for indirect reciprocity as neither grooming per se (GLM: β ±SE = 0.01 ±0.02; $F_{1,29}$=0.06, P=0.81, Power=0.17) nor difference in grooming (GLMM: β (95%CI) = -0.11 (-0.96 – 0.76), P=0.78, Power=0.41) by third parties to former food owners were contingent upon the previous FGS of second parties.

Negative reciprocity: Aggression before a session did not decrease FGS (mean with aggression (±SEM)= 0.15 (±0.09), mean without aggression= 0.24 (±0.02); GLMM: β ±SE = -0.38 ±0.67; LR=16.74, df=1, P=0.74, Power=0.13) nor did FGS influence aggression after a sharing session (mean before aggression (±SEM)= 0.50 (±0.50), mean before no aggression= 0.24 (±0.02); GLMM: β ±SE = 1.47 ±1.96; LR=0.85, df=1, P=0.53, Power=0.09). Thus, no effects of aggression on food sharing and vice versa were found, but the power of these models was very low, due to the rareness of aggression.

These results are summarized in Figure 3-1 a) – f). There were no qualitative differences between the two measures of FGS.

Figure 3-1: Short-term contingencies of grooming, food sharing and aggression among the chimpanzees. The upper row shows the influence on food-getting success (*only tolerated transfers*) during a sharing session of previous a) grooming by the approacher, b) differences in grooming by the approacher, i.e. did the approacher groom the owner more or less than usual and c) aggression by the approacher, within one hour *before* a sharing session. Conversely, the lower row shows the influence of food-getting success during a sharing session on subsequent d) grooming by the approacher, e) differences in grooming by the approacher, i.e. did the approacher groom the owner more or less than usual and f) aggression by the approacher, within one hour *after* a sharing session. Boxplots show median lines and quartiles. The plotted lines are the ones estimated by a simple linear regression model. None of the effects were significant (see text).

Bonobos

Positive reciprocity: Among the bonobos, food-getting success was significantly increased by previous grooming (mean with grooming ($\pm$SEM)= 0.21 ($\pm$0.12), mean without grooming= 0.06 ($\pm$0.06); GLM: $\beta \pm$SE = 3.37 $\pm$1.78; $F_{1,59}$=5.30, P<0.05, Power=0.35) and increased with a statistical trend by differences in DCI of grooming (GLM: $\beta \pm$SE = 2.10 $\pm$1.06; $F_{1,59}$=3.34, P=0.07, Power=0.76). However, these results were only found with FGS based on tolerated transfers, the results for FGS including forced transfers were not significant (*Grooming yes/no*: mean with grooming ($\pm$SEM)= 0.25 ($\pm$0.13), mean without grooming= 0.26 ($\pm$0.06); *Difference in DCI*: GLM: $\beta \pm$SE = 1.04 $\pm$1.00; $F_{1,59}$= 0.27, P=0.61, Power=0.06; GLM: $\beta \pm$SE = 0.92 $\pm$0.74; $F_{1,59}$= 2.38, P=0.13, Power=0.79). In turn, food-getting success did not influence subsequent grooming (mean before grooming ($\pm$SEM)= 0.11 ($\pm$0.04), mean before no grooming= 0.06 ($\pm$0.02); GLMM: $\beta \pm$SE = 0.72 $\pm$0.58; LR=1.43, df=1, P=0.28, Power=0.29) nor deviation from DCI after a session (GLMM: β (95%CI) = -0.05 (-0.30 – 0.20), P=0.72, Power=0.21). Thus, some evidence for short-term contingency was found among the bonobos, but only for an effect of grooming on sharing (and probably not vice versa, although the power of these models was low) and only for tolerated transfers.

Negative reciprocity: FGS of tolerated transfers was not significantly decreased by previous aggression (mean with aggression ($\pm$SEM)= 0.05 ($\pm$0.04), mean without aggression= 0.13 ($\pm$0.03); GLMM: $\beta \pm$SE = -1.37 $\pm$0.79; LR=55.35, df=1, P=0.81, Power=0.21), however, FGS including forced transfers was (mean with aggression ($\pm$SEM)= 0.13 ($\pm$0.06), mean without aggression= 0.30 ($\pm$0.04); GLM: $\beta \pm$SE = -1.04 $\pm$0.60; $F_{1,135}$= 4.20, P<0.05, Power=0.43). In turn, FGS did not influence subsequent aggression (mean before aggression ($\pm$SEM)= 0.02 ($\pm$0.02), mean before no

aggression= 0.09 (±0.02); GLMM: β ±SE = -1.71 ±1.37; LR=2.24, df=1, P=0.20, Power=0.26). Thus, there was some evidence for retaliation as aggression decreased the chance of taking food by force, but no evidence for punishment (although power here again is low). These results are summarized in Figure 3-2.
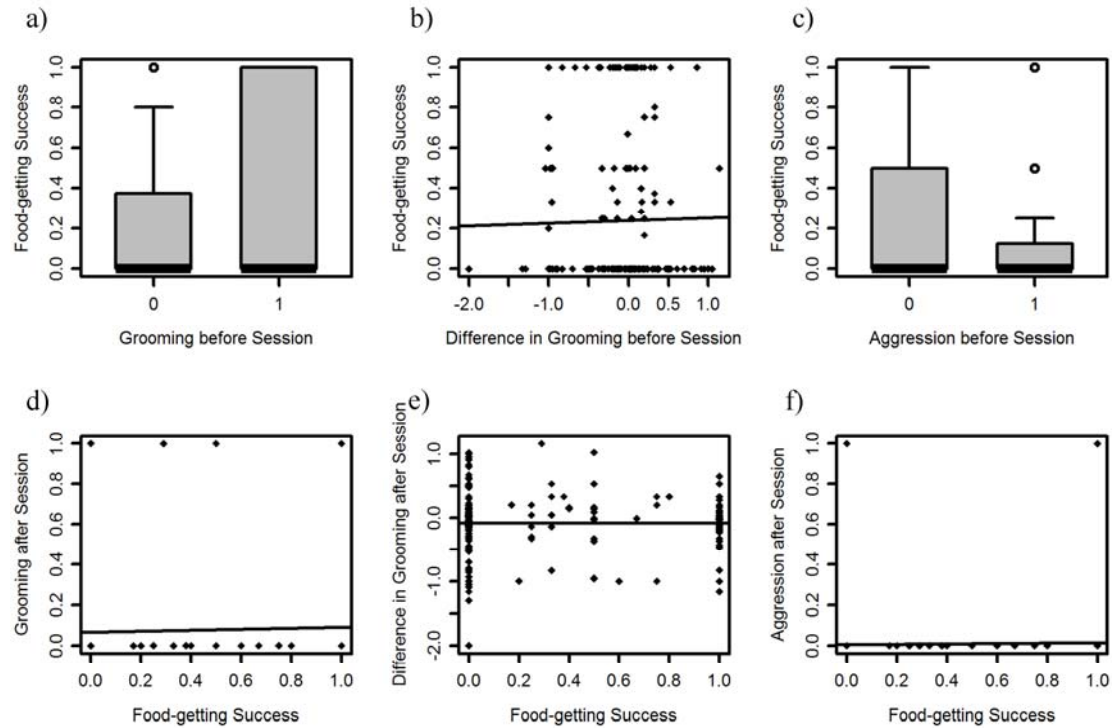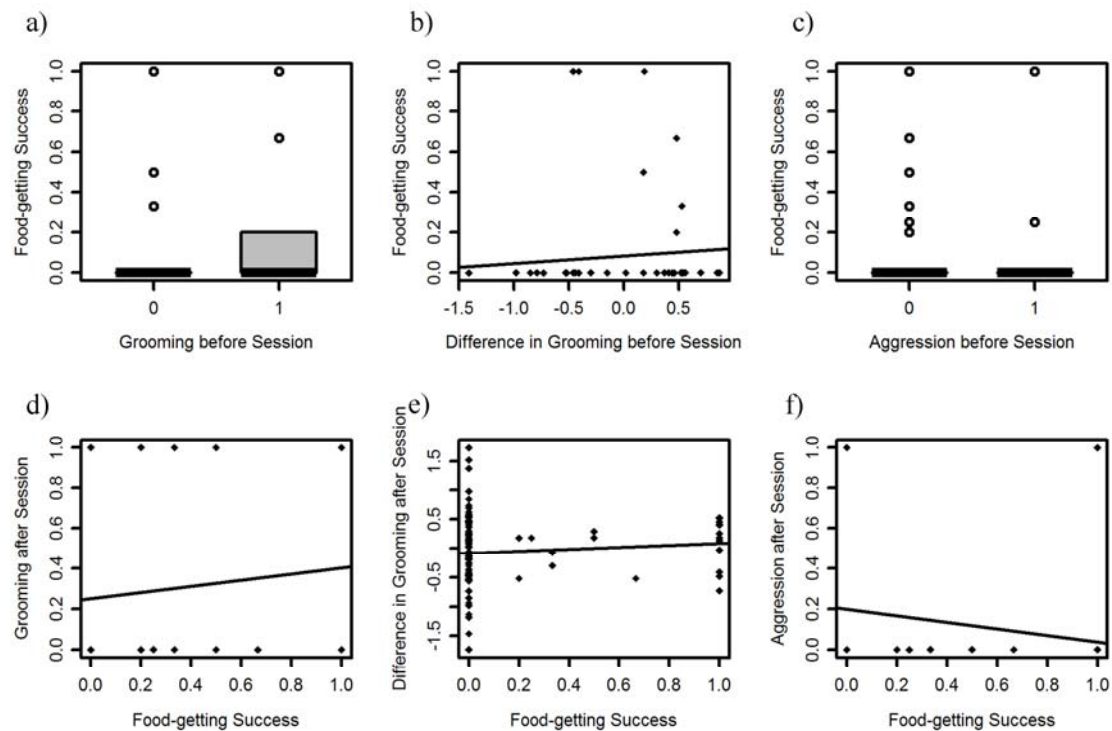

Figure 3-2: Short-term contingencies of grooming, food sharing and aggression among the bonobos. The upper row shows the influence on food-getting success (*only tolerated transfers*) during a sharing session of previous a) grooming by the approacher, b) differences in grooming by the approacher, i.e. did the approacher groom the owner more or less than usual and c) aggression by the approacher, within one hour *before* a sharing session. The lower row shows the influence on food-getting success during a sharing session on subsequent d) grooming by the approacher, e) differences in grooming by the approacher, i.e. did the approacher groom the owner more or less than usual and f) aggression by the approacher, within one hour *after* a sharing session. Plots are the same as in Figure 3-1. Significant effects were found for a) and b). An effect for c) was only found for FGS including forced transfers. No significant effects were found for d)-f) but the effects do go into the expected direction and statistical power of the models was low

Discussion

The only evidence for short-term contingencies we found was that bonobos had higher food-getting success if they groomed the food owner previously, but only for tolerated food transfers. Since all food transfers among the bonobos were passive (Jaeggi et al. 2010), this indicates that previous grooming selectively increased the food owners tolerance towards the approacher thus leading to decreased resistance and a higher chance of being allowed to take food. There was no difference between the two variables of grooming (did the approacher groom the owner yes or no; did the approacher groom the owner more or less than usual), indicating that the effect was not driven by a calculation of exchanged services but only by the act of grooming per se. The fact that sharing did not lead to more subsequent grooming suggests that being allowed to take food does not increase the motivation to groom, possibly because the former service is passive while the latter is active. Hence the effect only works the other way around. Since grooming is well known to increase endorphin levels in the groomee (Dunbar 2010), a proximate mechanism for this effect is easily found. Thus, we define "grooming effect" as a short-term increase in tolerance towards the groomer, which can lead to contingent reciprocity, given the possibility of exchange after grooming. On a cognitive level, the grooming effect thus requires some memory in order to be partner specific (de Waal 1997), but no mental scorekeeping or calculation. The fact that no grooming effect could be observed in the chimpanzee group may indicate that sharing tolerance was already at ceiling level. Hence, grooming effects could not override long-term tolerance due to symmetry-based reciprocity among the chimpanzees.

We suggest that almost all positive results of naturalistic studies testing short-term contingencies can be explained by the grooming effect (Seyfarth and Cheney 1984;

Hemelrijk 1994; de Waal 1997; Koyama et al. 2006; Table 3-1). Unfortunately none of these studies tested the effect the other way around, i.e. whether another service leads to more subsequent grooming, which could have allowed further scrutiny of the proximate mechanism. Future naturalistic studies testing for short-term contingency in other services, e.g. support after food sharing might help separating the grooming effect from other possible mechanisms for short-term contingencies. The lack of possibility for grooming effects may be one reason why more artificial experimental studies with lower ecological validity hardly ever found a positive effect (Table 3-1). Some of the results of studies that did find contingent reciprocity in the absence of grooming can still be explained by cognitively relatively simple mechanisms such as attitudinal reciprocity (de Waal 2000; de Waal and Berger 2000; Hauser et al. 2003). Only one study thus may infer calculated reciprocity (Dufour et al. 2009), suggesting that while maybe not beyond the cognitive capacities of primates, such calculative types of exchange are probably absent in nature and the fact that they may be elicited in artificial experiments may show the species' potential rather than its typical behavior (Noë 2006; Jaeggi et al. in press).

While most animals, and in particular primates engage in long-term stable relationships within which services are exchanged in a symmetrical way (Brosnan and de Waal 2002; Silk 2002), more contingent forms of reciprocity may only be necessary when interacting with relative strangers, with whom the chances of re-interacting are low and the temptation to cheat are thus high. Thus, calculated exchanges probably represent the basis of trade in humans (Brosnan and Beran 2009) and may only have arisen, or at least become a prominent feature of human interactions, when people started to engage in trade. Hence, regular use of calculated reciprocity may not date

back much earlier than the first archeological evidence for long-distance trade of raw materials in the Pleistocene (Klein 1999).

There was no evidence for punishment or retaliation in either species. Although it could be argued that our statistical power was too low to detect such effects, the fact that aggression was very rare after sharing sessions already indicates that punishment is not a prominent feature of sharing interactions. Furthermore, the long-term analyses (Appendix 3-1) also do not indicate a role of aggression in maintaining sharing generosity, contrary to earlier claims (de Waal 1989). These results indicate that chimpanzees and bonobos in this study did not have strong expectations about sharing interactions and were not outraged when not being allowed to take food. In contrast, strong sharing norms exist in all human societies, although actual physical punishment may also be relatively rare (Gurven 2004). These stronger expectations with regard to food sharing can be explained by the high interdependence of foragers where each family may depend on food subsidies from others on a majority of days (Gurven and Hill 2009). However, it is possible that sharing expectations among primates are higher when individuals cooperated to produce a food source such as in hunting in the wild (Boesch and Boesch 1989) or cooperation experiments in captivity (de Waal and Berger 2000).

We found no evidence that third parties groomed former food owners depending on their sharing generosity to others. (In fact, there was also no indication that third parties groomed former food owners more *regardless* of their sharing generosity, thus not confirming the hypothesis that owning food per se makes individuals socially more attractive (Moore 1984; see Appendix 3-2)). Hence, we conclude that third parties do not have expectations about the sharing generosity of others and indirect reciprocity is

unlikely to occur among chimpanzees in this context. Theoretical considerations and models indicate that direct reciprocity should prevail over indirect reciprocity as long as direct experience is cheap and chances of re-interacting are high (Nowak 2006). Thus, indirect reciprocity only becomes an important force in the evolution of cooperation when group sizes are large and the chances for direct reciprocity small (Roberts 2008), which is clearly not the case in zoo apes. During human evolution, indirect reciprocity possibly only arose as a response to increasing group size as well as the fission-fusion nature of foraging societies, which decreased the chances for direct experience with any potential cooperation partner (Alexander 1987; Kaplan et al. 2009).

In summary, we conclude that the observed short-term contingencies can be explained by a simple proximate mechanism, the grooming effect, which leads to selectively increased tolerance towards the former groomer, thus allowing more food transfers. The grooming effect, rather than calculated exchanges, may explain most of the short-term contingencies observed among non-human primates, although calculated exchanges are probably not beyond the cognitive capacities of (at least some) primates. Thus we conclude that long-term exchange is more common and more important among non-human primates while calculative types of exchange may only have arisen in humans with the need to engage in trade with relative strangers. Similarly, punishment and indirect reciprocity do not seem to be part of the food sharing reciprocity system of chimpanzees and bonobos and among humans are related to increased interdependence and group size of forager societies.

Chapter 4: On the psychology of cooperation in humans and

other primates: Combining the natural history and experimental

evidence of prosociality

In any given species, cooperation involves prosocial acts that usually return a fitness benefit to the actor. These acts are produced by a set of psychological rules, which will be similar in related species if they have a similar natural history of cooperation. Prosocial acts can be (i) *reactive*, i.e. in response to specific stimuli, or (ii) *proactive*, i.e. occur in the absence of such stimuli. We propose that reactive prosocial acts reflect sensitivity to (a) signs and signals of need and (b) the presence and size of an audience, as modified by (c) social distance to the partner or partners. We examine the evidence for these elements in humans and other animals, especially non-human primates, based on the natural history of cooperation, quantified in the context of food sharing, and various experimental paradigms. The comparison suggests that humans share with their closest living relatives reactive responses to signals of need, but differ in sensitivity to signs of need and cues of being watched, as well as in the presence of proactive prosociality. We discuss ultimate explanations for these derived features, in particular the adoption of cooperative breeding as well as concern for reputation and costly signalling during human evolution.

Introduction

Cooperative and altruistic behaviours can be favoured by natural selection if they increase the inclusive fitness of the actor (see Brosnan and Bshary in press; Lehmann and Rousset in press). The conditions under which this is the case are now well known (ibid.). However, which proximate mechanisms make an actor engage in such behaviours is less well understood. Here we focus on the *prosocial acts*, i.e. acts of help or assistance to others (Silk 2007), which together constitute cooperative and altruistic behaviour as defined by Brosnan and Bshary (in press). We propose that these acts are regulated by a set of psychological rules (henceforth: *rules*) that on average produce fitness-increasing behaviour. For instance, the rule to adjust prosocial acts to the recipient's need and preferentially directing them towards partners that reciprocated in the past is generally adaptive, because it maximises the return benefits through reciprocity (Trivers 1971), whatever exact cognitive or emotional mechanisms underlie it.

The idea that behaviour is produced by a set of rules follows the tradition of classical ethologists, who attempted to identify the corresponding intrinsic motivations and responses to extrinsic stimuli (Tinbergen 1951). In Figure 4-1, the intrinsic motivation is indicated by the intercept b, whereas the tendency to respond to extrinsic stimuli is indicated by the slope of the response a. Because natural selection works by modifying these rules over time, it is parsimonious to assume that they are similar in closely related species due to homology (de Waal 1991). Specifically, this view implies that humans and great apes are likely to have a similar psychology underlying prosocial acts. However, the psychology may change when one taxon evolves a different style of cooperation from that of its sister group, as we will argue for humans and great apes,

which could lead to convergent evolution with other taxa that evolved similar patterns of cooperation. Thus, the goal of this paper is to examine the psychological rules underlying prosocial behaviour in humans, based on natural history and experimental evidence, and to compare them with those of other primates, and in particular our closest living relatives, the great apes. The potential endocrinological correlates of these rules are discussed elsewhere (Soares et al. in press). We identify features in which humans generally differ from other animals and discuss hypotheses explaining the evolution of these features. (For the purpose of this chapter we ignore the large intraspecific variation documented in humans with respect to cooperative and anti-social behaviour (Gaechter et al. in press).)

The natural history of cooperation

Human foragers, whose ecology and social organisation are probably closest to the conditions under which our psychology evolved (Tooby and Cosmides 2005), systematically and frequently engage in various forms of cooperation. Thus, common prosocial acts include voluntary food sharing both with kin and non-kin, allo-maternal child care, division of labour, care for the sick, injured and elderly, information donation (teaching), cooperative hunting, collective warfare, etc. (Gurven 2004; Kaplan and Gurven 2005; Marlowe 2007; Gurven and Hill 2009; Hrdy 2009; Kaplan et al. 2009; Burkart and van Schaik 2010). Prosocial acts occur within family units, including pair-bonded partners and their offspring, and also among family units within local groups. Their pervasiveness suggests that they return high fitness benefits to actors.
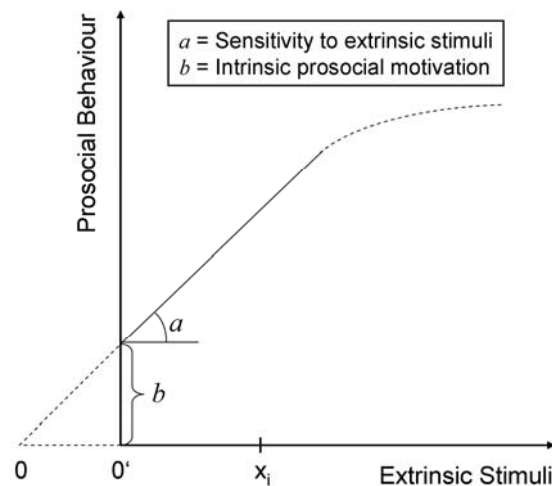
Figure 4-1: Prosocial behaviour as a function of extrinsic stimulus strength and intrinsic prosocial motivation. In humans, these stimuli can be perceived need of the recipient and/or the perceived presence and size of an audience. Social distance to the partner further modifies the prosocial response, i.e. at a given point x_i, kin, reciprocating partners or in-group members will generally elicit a higher prosocial response. Thus, prosocial behaviour in response to these stimuli may be called *reactive*. Eventually, the response will reach ceiling levels, as indicated by the dashed curve. If the intrinsic motivation b is greater than zero, prosocial behaviour may occur even in the absence of such stimuli and can thus be called *proactive*. However, since in practice it may be impossible to exclude all extrinsic stimuli, experiments trying to do so may measure prosociality at 0' rather than 0 and proactive thus refers to either a high intrinsic motivation or a high sensitivity to the remaining stimuli, as indicated by the dashed lines leading to 0. Ultimately, natural selection can work by changing the sensitivity to stimuli, a, and/or the intrinsic motivation, b, depending on the average certainty of return benefits to the actor. Humans have probably acquired a greater intrinsic prosocial motivation, as well as a higher response to extrinsic stimuli since their divergence from great apes

Among great apes, cooperation is less common and prosocial acts are less pervasive (Melis and Semmann in press). Food sharing is generally reluctant and rarely active, even among kin (Figure 4-2, discussed in detail below), there is little evidence

for teaching (reviewed by Humle et al. 2009; Jaeggi et al. 2010a) and allo-maternal

child care is virtually absent, as is care for the disabled beyond grooming (Hrdy 2009;

van Schaik and Burkart 2010). Among chimpanzees, the most common forms of

cooperation involve closely bonded males, such as in mutual support in conflicts (Watts

2002; Gilby et al. 2009), cooperative hunting (Boesch and Boesch 1989; Boesch 1994;

Watts and Mitani 2002) and inter-community warfare (Manson and Wrangham 1991).

This indicates that prosocial acts among great apes on average yield lower fitness

benefits to actors, with the possible exception of chimpanzee males, who seem to profit

more from cooperation. Probably this is due to the relatively low average relatedness of

chimpanzees and the resulting reliance on direct reciprocity for many aspects of

cooperation (Langergraber et al. 2007; Langergraber et al. 2009), as well as the absence

of strong pair-bonds.

Species other than great apes show more parallels with humans with respect to

the natural history of cooperation. In particular, voluntary food sharing, teaching, allo-

maternal care and care for the injured are more common in cooperative breeders such as

callitrichid monkeys or social carnivores (Kühme 1965; Brotherton et al. 2001; Clutton-

Brock et al. 2001; MacDonald and Sillero-Zubiri 2004; Thornton and Raihani 2008;

Hrdy 2009; Burkart and van Schaik 2010). This indicates that cooperative breeders

enjoy higher return benefits from prosocial acts and are more prone to engage in them.

Could this similarity with humans reflect convergent evolution?

Humans can also be called cooperative breeders, since they show high levels of

infant care by older siblings, husbands, and grandmothers (reviewed by van Schaik and

Burkart 2010). In contrast, great ape females are independent breeders who receive no

help in rearing their young (Hrdy 2009). While most great apes, and in particular

females with offspring, are relatively solitary in order to avoid feeding competition (van Schaik 1999; Stumpf 2007), cooperative breeders typically form family groups, including at least one bonded pair and multiple offspring, both dependent and independent (Clutton-Brock 2002; Chapais 2008). Within this expanded kin network, prosocial acts should be under more positive selection and the underlying psychology could change accordingly. Thus, the Cooperative Breeding Hypothesis states that some convergent evolution between humans and other cooperative breeders explains the emergence of psychological and cognitive features in humans not shared by the other apes (Burkart et al. 2009; Hrdy 2009; Burkart and van Schaik 2010).

Humans may also differ from chimpanzees in two other important aspects of cooperation. Firstly, there is substantial *interdependence* among foragers, because the returns from individual foraging are smaller than the ones from cooperative foraging and hunting returns are large but so unpredictable that sharing became a survival necessity (Kaplan et al. 2009). Thus, a solitary human forager, in stark contrast to a solitary chimpanzee, is always worse off than a cooperative forager. Furthermore, the fission-fusion dynamics of foragers allow for considerable partner choice, thus restraining selfish tendencies due to the risk of losing valuable cooperation partners (ibid.). These two aspects combined caused the necessity to establish and maintain a cooperative reputation. Thus, non-cooperative individuals may face substantial costs imposed by the "moral community" (Boehm 1999) ranging from shunning over overt accusations to ostracism and violence (Boehm 1999; Gurven 2004; Marlowe 2009). These potentially high costs exerted by others on cheaters probably led to a hyper-awareness of the risk of being detected, i.e. a *conscience* (Trivers 1971; DeScioli and Kurzban 2009), functioning to anticipate others' reactions and thus avoid these costs.

Combined with large group sizes and the possibility to spread reputations through language as gossip in a fission-fusion society (Dunbar 2004), concern for reputation should thus have lead to an increased sensitivity to being watched by others. Secondly, individuals, and in particular men, may signal cooperative tendencies and their own qualities to large audiences in order to increase their chances of being chosen as cooperation partners or mates (Smith and Bliege Bird 2005). Thus, costly signalling theory also predicts sensitivity to the presence and size of an audience, in order to maximize the broadcasting efficiency of costly signals.

Hence, some aspects of human cooperation are probably homologous with our closest relatives, in particular with regard to mutualism and direct reciprocity (hunting, warfare, agonistic support) whereas others are better explained by convergence with cooperative breeders, probably due to increased kin networks and strong pair-bonds, and yet others are probably uniquely derived, viz. concern for reputation and the broadcasting of prosocial acts to large audiences. These aspects of the natural history of cooperation are likely to affect the psychological rules regulating prosocial acts.

Psychological rules underlying prosociality

As indicated in Figure 4-1, we propose that prosocial behaviour can be *reactive*, i.e. triggered by extrinsic stimuli (with a positive slope *a*); or *proactive*, i.e. in the absence of any obvious extrinsic stimuli, indicated by the intrinsic motivation *b*. Note that common definitions of altruism in other fields, such as in psychology (Batson 1991) or philosophy (Kitcher 1998) mainly refer to proactive prosociality and may not consider prosocial behaviour in response to explicit stimuli altruistic.

In general, the steepness of the response (*a*) will have been moulded by natural selection according to the average probability of return benefits to the actor. As both kin selection and reciprocity theory predict that prosocial acts should be adjusted to the recipient's need in order to achieve the greatest potential benefit (Hamilton 1964; Trivers 1971), actors should be sensitive to signals or signs of need. Note that responding to *signals* of need usually requires no special abilities, because they are directed at the actor and have specifically evolved in a form that most successfully elicited the desired response (Zahavi 1987). However, the ability to correctly read *signs* of need (not directed to actor) may often depend on theory-of-mind capacities. Thus, actors with a well-developed theory of mind may be better at perceiving adequate situations for prosocial acts which should lead to a steeper slope *a*. Furthermore, the importance of maintaining a cooperative reputation and the opportunities for costly signalling predict that actors should be sensitive to the (perceived) presence and size of an audience (Trivers 1971; Smith and Bliege Bird 2005; DeScioli and Kurzban 2009; Earley in press). Hence, an increase in either perceived need and/or perceived signalling opportunities (along the x-axis of Figure 4-1) should lead to increased prosocial behaviour. Finally, the social distance to the recipient should function as a modifier of the prosocial response. Thus, all other things being equal (same x-value), close kin and reciprocating partners (friends) should elicit a higher prosocial response, because the average return benefit to the actor is greater.

Identifying psychological rules

In humans, the presence of prosocial behaviour in response to specific stimuli can be shown with so-called "titration experiments", by keeping all other stimuli

constant and only changing the one of interest. For instance, dictator games, in which a dictator can allocate any amount of received money to a potential recipient, can be played under varying conditions, e.g. including subtle cues of being watched (Haley and Fessler 2005; Rigdon et al. 2009). The increase in contribution when a dictator feels observed allows us to conclude that they are sensitive to having an audience, even though this sensitivity may be entirely subconscious.

A prosocial act in the absence of extrinsic stimuli may be called *proactive* prosociality (*b* in Figure 4-1). This is more controversial, since the notion that all extrinsic stimuli can be excluded in controlled experiments can be questioned (e.g. Trivers 2006; Bardsley 2008). Thus, it may be safer to assume that experiments take place at 0' rather than 0 (see Figure 4-1), where extrinsic stimuli have been excluded or controlled for as much as possible, but some residual stimuli may remain. Hence there may be a grey area where prosocial acts can be either provoked by a high intrinsic motivation and/or a very strong response to subtle stimuli (high *a* in Figure 4-1). In particular, in the case of an audience, the awareness of the risk of detection may be so strong that actors respond prosocially to subtle cues of being watched or just the *idea* of being watched. In this view, conscience thus functions to anticipate reactions by a potential audience (Trivers 1971; DeScioli and Kurzban 2009). Similarly, in the case of need, actors could respond to just the slightest signs of need in a potential recipient if their theory of mind capacities are well developed, or they could respond to the *idea* of the recipient being in need. If this is the case, many humans may never actually reach 0 level, i.e. no experimental setting can exclude all social influences and make actors decide out of purely selfish considerations (Trivers 2006).

Among animals, and in particular non-human primates, similar experimental approaches have been followed. Provisioning experiments were often designed to reflect economic games played with humans, and have mainly focused on *proactive* prosociality. A fundamental constraint on them is that they cannot be played anonymously, but nonetheless, if prosocial behaviour occurs in the absence of or regardless of any measurable stimuli from the recipients, the plausible conclusion would be to infer a high intrinsic motivation (*b*), or a very high sensitivity to residual stimuli (*a*). Other experiments investigated prosocial acts in response to signs or signals of need, such as so-called targeted helping experiments. Table 4-1 gives an overview over the types of experiments we discuss below, as well as their main findings. In all these experiments, one should be aware of the risk of false positives or false negatives due to possible confounding effects on the subjects' behaviour. This risk is especially high in experiments with low ecological validity, since they may not be understood by the subjects in the same way as conceived by the experimenters. Hence, one should examine the pattern of results as a whole, without over-emphasising single studies, and validate them through consistency with the natural history.

Another line of evidence we therefore examine is naturally occurring food sharing. Defined as the tolerated transfer of food from A (the owner) to B (the recipient), food sharing is a common form of prosocial behaviour among primates (Feistner and McGrew 1989; Brown et al. 2004; Rapaport and Brown 2008). However, food sharing is clearly not homogeneous among primates with respect to the underlying psychology. In most species transfers are mainly passive, even among kin, while in others food owners may actively promote transfers by "offering" (Feistner and McGrew 1989), thus showing stronger prosocial dispositions. Here we present a quantification of

these ways in which food is transferred (Figure 4-2, see Appendix 4-1 for operational definitions), focussing on the best-studied taxa: great apes, capuchins and callitrichids (see Appendix 4-2 for complete list of species). In particular, we will discuss food offering, i.e. transfers initiated by the owner in the absence of begging, as reflecting *proactive* prosociality and active sharing upon begging as reflecting *reactive* prosociality, in response to signals of need. Tolerated taking or *passive* sharing, the most common form of food sharing among primates (Figure 4-2), is more ambiguous with regard to the underlying psychology since the lack of overt action could represent no prosocial response or an explicit absence of a negative response to the beggar. However, parsimony suggests that no overt action mostly reflects the absence of a psychological response.

Evidence for psychological rules

This section summarizes empirical evidence for the proposed psychological rules underlying prosocial acts in humans and other primates. First, we examine reactive prosociality (1), in response to perceived need (a) or audience (b) and as modified by social distance to the recipient (c). Then we discuss the possibility of proactive prosociality (2), i.e. in the absence of extrinsic stimuli. In each subsection we first present the evidence on (i) humans and then (ii) on primates, as inferred from experimental evidence and food sharing. The primate evidence focuses on great apes as our closest living relatives, and in particular chimpanzees as the best studied species, but other species, in particular capuchin monkeys and callithrichid monkeys are mentioned throughout to illustrate parallels with humans.

Table 4-1: Summary of experimental outcomes measuring prosocial tendencies in primates

Paradigm	Chimpanzees	Macaques	Capuchins	Callitrichids
Provisioning games	Negative[1,2,3,4]	Positive[10], negative[11-13]	Positive[14-16]	Positive[20-22] Negative[23,24]
Unilateral cooperation	Tends to break down[5,6]		Reciprocal[17,18]	Reciprocal[25] Sustained[26]
Targeted helping	Positive[7-9]		Positive[19]	

[1,2,3,4](Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008; Yamamoto and Tanaka 2010), [5,6](reviewed by Snowdon and Cronin 2007; Warneken and Tomasello 2009), [7-9](Warneken and Tomasello 2006; Warneken et al. 2007; Yamamoto et al. 2009), [10](but no control for simpler explanations: Massen et al. 2010), [11-13](Mason and Hollis 1962; Colman et al. 1969; Schaub 1996), [14-16](de Waal et al. 2008; Lakshminarayanan and Santos 2008; Takimoto et al. 2010), [17,18](de Waal and Berger 2000; Hattori et al. 2005), [19](Barnes et al. 2008), [20-22](Hauser et al. 2003; Burkart et al. 2007; Cronin et al., in rev.), [23,24](Cronin et al. 2009; Stevens 2010), [25](Hauser et al. 2003), [26](Cronin and Snowdon 2008)

Reactive prosociality

a) Need

(i) Humans routinely respond with prosocial acts to the need of the recipient as signalled by the latter, e.g. through an outstretched hand in a begging gesture and/or vocalizations, and start doing so at young ages (Eisenberg and Mussen 1989; Brownell et al. 2009). This is illustrated by the frequent reactive food sharing of young children (Figure 4-2). The underlying motivation is probably empathy or sympathy (Trivers 1971; Eisenberg and Mussen 1989; Silk 2007; de Waal and Suchak in press). Furthermore, even in the absence of explicit *signals* of need (in the form of a directed solicitation), an actor can respond to *signs* of need. For instance, if an individual is trying to reach an object, an actor may respond by retrieving and handing over the object (Warneken and Tomasello 2006). Note that the correct interpretation of such signs of need depends on specific theory of mind capacities particularly well developed in humans (Burkart et al. 2009), which may explain why in children helping is elicited faster and in a broader range of contexts than in chimpanzees (Warneken and Tomasello 2006; Warneken et al. 2007).

(ii) Among great apes, and in particular chimpanzees, signals of need can be seen in solicitation of grooming (Pika and Mitani 2006), of agonistic support (de Waal 1982), or of food. Begging for food may sometimes elicit *reactive* sharing, but most often there is no overt response and food is shared passively (if at all), suggesting a low sensitivity to need (Figure 4-2). Indeed, reactive sharing may often serve to get rid of the beggar, even the actor's own offspring, by giving scraps while withholding more valuable food (Kuroda 1984; Bard 1992; Ueno and Matsuzawa 2004), thus reflecting selfishness rather than prosociality. However, among adults, and in particular chimpanzee males, reactive sharing is somewhat more common (Figure 4-2) and may sometimes include large quantities of meat (Boesch and Boesch 1989; D. Watts pers.comm.), suggesting higher sharing motivation.

Great apes, especially chimpanzees, are known to have relatively well-developed theory of mind capacities (Call and Tomasello 2008) and could thus be expected to read and respond to recipient need. Yet, crucially, *signs* of need, such as approaching and peering at a food owner without begging hardly ever leads to sharing (Kuroda 1984; Jaeggi et al. 2008; Jaeggi et al. 2010b), suggesting that explicit signals are required for a prosocial response.

We now turn to the experimental evidence. Begging did not induce food donation in provisioning games among chimpanzees (Silk et al. 2005; Jensen et al. 2006), which may reflect low sensitivity to these signals if they are not made in immediate proximity. However, helping behaviour in response to explicit signals of need has been reported for chimpanzees (Warneken and Tomasello 2006; Warneken et al. 2007; Yamamoto et al. 2009) and capuchin monkeys (Barnes et al. 2008) in targeted helping experiments (Table 4-1). Crucially, signs of need such as struggling to solve a

task (Yamamoto et al. 2009) or reaching for an object without calling the subjects name (Warneken et al. 2007) mostly did not induce helping in chimpanzees, unless they were well enculturated by humans (Warneken and Tomasello 2006).

Cooperative breeders, such as callitrichids and social carnivores may use signals of need in the form of specific begging calls which usually increase begging success (Kühme 1965; Feistner and McGrew 1989; Mech et al. 1999; Manser and Avey 2000; Brown et al. 2004). There is also good experimental evidence that the response to these vocalizations are adjusted to the beggar's skill level (Thornton and McAuliffe 2006; Humle and Snowdon 2008a). Signs of need (reaching) also did not induce a prosocial response in callithrichids (Burkart et al. 2007; Cronin et al. 2009). Thus, cooperative breeders generally show reactive prosociality to signals of need, but not to signs of need.

Taken together, the most striking result is not the response to signals of need, but rather its often reluctant nature or even absence in many species, in particular in the food-sharing context (Figure 4-2, Appendix 4-2), as well as the unresponsiveness to *signs* of need. These findings and the fact that, at least among chimpanzees, theory of mind capacities are better developed in competitive rather than cooperative situations (Hare and Tomasello 2004) suggest that in this species prosocial responses to signals and signs of need have not been under the same positive selection as in humans, i.e. that the slope *a* in Figure 4-1 is shallower.

b) Audience

(i) The (perceived) presence and size of an audience can increase prosocial behaviour among humans in natural situations (Smith and Bliege Bird 2005) as well as in various experiments, where subtle eye cues or actual audiences increased

contributions in dictator games (Marlowe 2004; Haley and Fessler 2005; Rigdon et al. 2009), public goods games (Milinski et al. 2002; Bateson et al. 2006; Burnham and Hare 2007) and trust games (Fehr and Schneider 2010). This adjustment to a potential audience may be largely unconscious (cf. Bateson et al. 2006). Finally, the fact that some of the effects are entirely driven by men (e.g. Rigdon et al. 2009) may indicate costly signalling while the response to more explicit reputation incentives (e.g. Fehr and Schneider 2010) may indicate a general concern for reputation.

(ii) Among animals, sensitivity to presence of an audience is expected when individuals have to maintain a cooperative reputation or advertise their own qualities in the face of considerable partner choice. While this has been nicely shown in fish (Bshary and Grutter 2006), only anecdotal observations suggest that chimpanzee males rising in rank may use food sharing to signal generosity to the whole group (de Waal 1982). The number of beggars positively affects the amount of food shared among chimpanzees and bonobos (Fruth and Hohmann 2002; Gilby 2006), but this has been interpreted as reflecting increased harassment rather than signalling generosity. So far, no controlled experiments have been done to investigate the role of an audience on prosocial behaviour.

A precondition for audience effects on cooperative behaviour is that the potential audience actually attends to interactions between others and uses this information to build reputations. There is much evidence that animals eavesdrop on others' interactions (e.g. Bshary and Grutter 2006), but amongst primates eavesdropping mainly concerns dominance interactions (Bergman et al. 2003) or sexual behaviour (Crockford et al. 2007) rather than prosocial acts (see Earley in press). Recent experiments have shown that chimpanzees, but not capuchins (Brosnan and de Waal

2009), can learn to distinguish between a prosocial and a selfish human experimenter (Russell et al. 2008; Subiaul et al. 2008), suggesting that the audience can build prosocial reputations. However, as noted above, no experiments have tested whether actors respond to a greater number of observers with more prosociality. Furthermore, there is hardly any evidence that non-cooperative behaviour is punished by others (Jensen in press). Thus, more studies are clearly needed to investigate audience effects in nonhuman primates in the context of prosociality.

c) Social distance

(i) In humans, all other things being equal, partners with whom the actor has a strong affiliative bond based on either kinship or friendship can elicit more prosocial acts than enemies or neutral persons (e.g. Birch and Billman 1986; Eisenberg and Mussen 1989; Majolo et al. 2006) and in-group members are favoured over out-group members (Goette et al. 2006; Fehr et al. 2008). There is also clear evidence that these prosocial acts are further influenced by the recent history of interactions, taking e.g. indebtedness into account (e.g. Eisenberg and Mussen 1989). The underlying emotions here are probably feelings of gratitude or guilt (Trivers 1971), which can thus have short-term effects on perceived social distance.

(ii) Many animals have some way of recognizing or preferentially interacting with their close kin if they have the opportunity to do so (Chapais 2006; Silk 2006). Furthermore, unrelated individuals in many species of primates form long-term social bonds, called friendships (Silk 2002), characterized by reciprocal exchange of grooming and other social commodities such as coalitionary support or food sharing (Brown et al. 2004; Schino 2007; Schino and Aureli 2008; Schino and Aureli 2009; Jaeggi and van Schaik in review). Hence, there is a clear preference among primates to direct prosocial

acts to kin or reciprocating partners (friends). The recent history of interactions, i.e.

indebtedness, may also sometimes be taken into account (e.g. Hemelrijk 1994; de Waal

1997; de Waal 2000).

Nonetheless, controlled experiments in which subjects were given a choice to act

prosocially towards a relative, friend or a neutral partner were largely inconclusive.

Chimpanzees did not provide more food to kin than to non-kin (Jensen et al. 2006;

Yamamoto and Tanaka 2010) and neither did macaques (Schaub 1996). Only capuchin

monkeys differentiated between kin, familiar and unfamiliar partners (de Waal et al.

2008). Thus, even though natural observations clearly indicate partner specificity in

prosociality, as predicted by kin selection or reciprocity, many provisioning experiments

surprisingly indicated a complete absence of prosociality. This may again indicate that

prosocial acts among many primates, even to relatives or friends, need to be elicited by

immediate and salient stimuli, such as continuous begging (cf. Yamamoto and Tanaka

2009b), which was not possible in these experiments. This notion is supported by the

fact that among most primates virtually all food sharing, even with infants, is in

response to begging (Figure 4-2, Appendix 4-2).
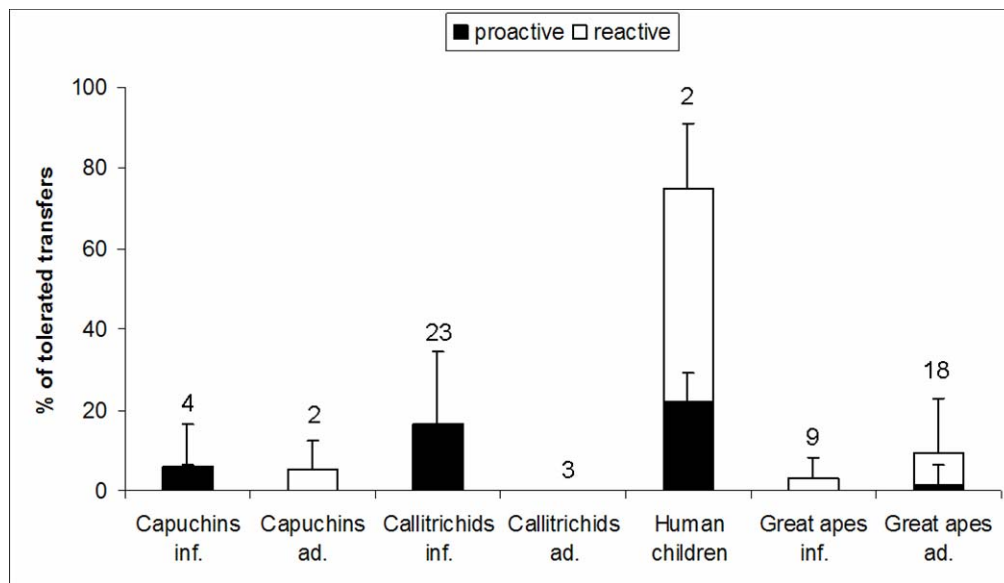
Figure 4-2: Percentages of all tolerated food transfers among different primate species in which the owner shared *proactively* (offering) or *reactively* (active giving or facilitated taking upon begging). The remaining transfers were *passive* (tolerated taking). See Appendix 4-1 for operational definitions and Appendix 4-2 for a full reference list including additional species. Bars represent means of different studies, i.e. the percentage of each type of transfer from each study, or independent study group is counted as one data point. The numbers above the bars indicate the number of independent data points contributing to these means. Inf.= sharing with infants, ad.= sharing among adults

Proactive prosociality

(i) Proactive sharing or helping occurs in experiments with human children (Birch and Billman 1986; Rao and Stewart 1999; Warneken and Tomasello 2006), but it is difficult to exclude possible signs or signals of need in these paradigms. In one-shot dictator games in which anonymity and large social distance are ensured as much as possible and the need of the recipient is unknown, the average contributions are always above zero (although many players actually do give zero), indicating that at least a subset of individuals is prosocial in the absence of any stimuli (see Camerer 2003, Table

2.3 for a compilation of various studies). These experiments thus led to the conclusion that humans are at least occasionally motivated by other-regarding preferences (Camerer 2003).

(ii) Among non-human primates, proactive prosociality can be seen in food offering, i.e. when food owners initiate sharing in the absence of begging or other signs of interest by the recipient (Feistner and McGrew 1989). Offering has been reported occasionally for a number of species (see Figure 4-2, Appendix 4-2 for species not in the figure). However, regular offering is only seen among callitrichids, where parents and helpers give specific food calls to invite transfers to the infants (Figure 4-2). This indicates a strong motivation to share and suppression of own feeding motivations among callitrichids, which is further supported by the facts that preferred food is more likely to be offered (Feistner and Chamove 1986; Ferrari 1987), animals offer more when infants are out of sight (e.g. Ferrari 1987; contrary to capuchins: de Waal et al. 2008), and they offer food to other adults (Rapaport 2001) or even to infants of different species (Feistner and Price 1999). This strong sharing motivation among callitrichids is in line with the high motivation to carry infants (Hrdy 2009), despite the substantial cost associated with it (Schradin and Anzenberger 2001). Non-primate cooperative breeders may show similarly high motivations to help and share (Kühme 1965; Clutton-Brock et al. 2001).

Since proactive prosociality has been claimed for humans mainly on the basis of non-zero contributions in dictator games (Camerer 2003), similar games have been designed to test primates (see provisioning games in Table 4-1). In chimpanzees, four studies did not find any evidence for proactive prosociality, even in mother-offspring dyads (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008; Yamamoto and Tanaka

2010). In macaques there was also hardly any evidence for prosociality in provisioning games (Mason and Hollis 1962; Colman et al. 1969; Schaub 1996). (A recent study did report provisioning from dominants to subordinates (Massen et al. 2010). However, it did not find sharing in the opposite direction, and the experimental set-up did not rule out the simpler explanation that dominants prefer to sit close to subordinates (e.g. so as to induce being groomed), whereas the latter avoid the former (to avoid aggression). Furthermore, generous behaviour by dominants is in stark contrast to the natural history of this despotic species, where most grooming is directed up the hierarchy (Schino & Aureli 2008) and food sharing is virtually absent (Jaeggi & van Schaik in review). Hence the null model of no proactive prosociality is not convincingly rejected). In capuchin monkeys, mainly positive evidence has been reported (de Waal et al. 2008; Lakshminarayanan and Santos 2008; Takimoto et al. 2010). In callitrichids, some studies report positive evidence for common marmosets (Burkart et al. 2007) and cotton-top tamarins (Hauser et al. 2003; Cronin et al. in rev.), but others do not (Cronin et al. 2009; Stevens 2010). Because the positive evidence is less easily explained away and here is consistent with the natural history, the preliminary conclusion that callitrichids show proactive prosociality seems warranted.

A high intrinsic motivation to act prosocially may also be expressed in so-called unilateral cooperation games (Table 4-1), in which only one of two individuals is rewarded for a task solved by both. In these games, cooperation tends to break down among chimpanzees (reviewed by Warneken and Tomasello 2009). Among capuchins, unilateral cooperation works if the role of recipient is alternated (de Waal and Berger 2000; Hattori et al. 2005), allowing for immediate reciprocation. Among tamarins, in contrast, it is sustained over long periods without alteration of rewards or signals of

need (Cronin and Snowdon 2008). Thus, a high intrinsic prosocial motivation apparently allows them to keep cooperation going in the absence of immediate rewards.

Discussion

Methodological issues

Before drawing conclusions from the evidence reviewed above it is important to eliminate potential confounding effects. In particular, we discuss the possibilities that primates may be more prosocial in non-food vs. food tasks and that rearing and housing conditions may affect levels of prosociality.

Firstly, it has been suggested that prosociality is more pronounced in non-food contexts (e.g. de Waal et al. 2008; Warneken and Tomasello 2009; Yamamoto and Tanaka 2009b) perhaps due to an obsession with food and the associated lack of inhibitory control in provisioning experiments. The evidence for non-food prosociality among chimpanzees includes targeted helping (Table 4-1) as well as other contexts such as adoption of orphans (Boesch et al. 2010). However, in these contexts prosociality is also mainly reactive, thus not contradicting the main findings here. Furthermore, tool sharing by great ape mothers, a non-food context, seems to be equally reactive as food sharing, happening virtually only upon request by the infant (Hirata and Celli 2003b; Lonsdorf 2006; C. Sanz et al. in prep.; cf. Figure 4-2). Hence, the psychological regulation of prosociality seems similar in food or non-food contexts.

Secondly, rearing and housing conditions may affect subjects' performance in experiments (Boesch 2007). For instance, the degree of enculturation, through hand-rearing or daily interactions with animal keepers is likely to affect subjects' psychology.

In particular, since many prosociality paradigms reflect typical human interactions, sometimes with little ecological validity for the primates, enculturated individuals are more likely to grasp the idea of the paradigm. For instance, the subjects of Warneken et al. (2007) were housed in the chimpanzee sanctuary of Ngamba Island, where the chimpanzees receive their daily food in bowls which they have to actively *hand* to the keepers. This may well have influenced their performance in a very similar experiment in which they had to retrieve an object and hand it to a human experimenter (ibid.). This is not to say that the experimental results are flawed, but they may reflect the species' *potential* rather than species-typical behaviour. Thus, if enculturated chimpanzees can learn to be more prosocial, the conditions under which this is the case may help explain how our own species came to evolve in this direction, but it need not necessarily inform us about chimpanzee-typical prosociality.

Reconstructing the evolution of human prosociality

Despite these uncertainties, some general conclusions about similarities and differences in the psychological regulation of prosociality in the best-studied species can be drawn. These are summarized in Table 4-2. We infer the presence of three components with different evolutionary histories: one shared with other apes, especially chimpanzees, a second acquired due to the adoption of cooperative breeding and probably shared with other cooperative breeders, and a third one acquired uniquely due to living in large, fission-fusion societies with high interdependence amongst individuals.

Table 4-2: Summary of the main findings regarding the proximate regulation of prosocial acts in the best studied species

Rule	Humans	Chimpanzees	Capuchins	Callitrichids	Evoluationary status
Need[a]	++ (signs and signals)[e]	+ (signals)	+ (signals)	+ (signals)	homologous
Audience[b]	++	(-)	(-)	(-)	uniquely derived
Social distance[c]	++	+	++	+	homologous
Proactive[d]	++	--	+	++	convergence

[a-c] Do actors adjust prosociality to [a] the perceived need of the recipient, [b] the perceived presence and size of an audience, or [c] the social distance to the recipient?
[d] Do prosocial acts occur in the absence of obvious extrinsic stimuli, thus reflecting a high intrinsic prosocial motivation?
[e] Signs of need by the recipient, such as reaching for an object or struggling with a task, are not directed at the actor and probably require some theory of mind capacities to be correctly read; signals of need, such as begging or calling, on the other hand are explicitly directed at the actor
++ regular in experimental and natural context; + regular in at least one context; -- absent in both contexts; (-) possibly absent but no controlled experiments (cf. Table 4-1, Figure 4-2, text)

Humans are both regularly proactively prosocial, thus reflecting a high intrinsic prosocial motivation, and highly responsive to extrinsic stimuli. Chimpanzees, in contrast, are hardly ever proactively prosocial and their reactive prosociality generally depends on salient and immediate signals of need such as continuous solicitations (cf. Yamamoto and Tanaka 2009b). This agrees with the notion that chimpanzee cooperation among adults mainly rests on direct reciprocity, which is clearly indicated by the presence of long-term social bonds (friendships, Silk 2002) within which favours are exchanged symmetrically (e.g. Watts 2002; Mitani 2006) and by the low average relatedness within these cooperative relationships (Langergraber et al. 2007; Langergraber et al. 2009). Hence chimpanzees are a good example for both the scope and limits of cooperation based on direct reciprocity: The establishment of long-term friendships and the corresponding attachment allows chimpanzees to engage in various forms of cooperation such as cooperative hunting (Boesch and Boesch 1989; Boesch 1994), agonistic support (e.g. Watts 2002; Mitani 2006) and collective warfare (Manson

and Wrangham 1991). Thus, prosocial acts are particularly common among males, who profit most from cooperation (Boesch and Boesch 1989; Nishida et al. 1992; Watts 2002). On the other hand, cooperation is subject to opportunistic fluctuations (de Waal 1982; Gilby et al. 2009) and in experiments has difficulty getting started (Brosnan and Beran 2009; Brosnan et al. 2009; Yamamoto and Tanaka 2009a) or tends to break down in the absence of immediate rewards (reviewed by Warneken and Tomasello 2009) or explicit solicitations (Yamamoto and Tanaka 2009b). These difficulties of experimental reciprocity may further indicate that reciprocity among chimpanzees (and indeed most animals) is mainly symmetry-based rather than calculated (Brosnan and de Waal 2002), i.e. prosocial acts are averaged out on a long-term basis mediated by affiliative emotions rather than exchanged contingently in a tit-for-tat manner requiring substantial cognitive effort (Stevens and Hauser 2004; see discussion by Brosnan et al. this volume). While it is parsimonious to assume that human ancestors shared these aspects of cooperation based on direct reciprocity with chimpanzees, humans seem to have acquired several derived features, some of which may have evolved convergently with other taxa. These derived features combined to make human cooperation more stable relative to chimpanzees.

The regular proactive element of human prosociality almost certainly shared with callitrichids suggests that a high intrinsic prosocial motivation evolved convergently in cooperative breeders, probably because of the risk of neglect of unattended offspring (Hrdy 2009; Burkart and van Schaik 2010), and the need for active provisioning to maintain fast growth levels (Brown et al. 2004; Gurven and Hill 2009). This proactive element could also explain why teaching is more common among cooperative breeders (Rapaport 2006a; Rapaport and Brown 2008; Burkart and van

Schaik 2010) whereas great apes often do not take advantage of low-cost opportunities to teach (Hirata and Celli 2003b; Lonsdorf 2006; C. Sanz et al. in prep.; Jaeggi et al. 2010a). Furthermore, the adoption of cooperative breeding typically leads to the formation of family units, within which prosocial acts are dispensed more freely because they generally benefit close kin or pair-bonded partners (Chapais 2008; Hrdy 2009; Burkart and van Schaik 2010). Thus a high intrinsic prosocial motivation would not be counter-selected if applied within the family. Finally, within human societies kin networks extend far beyond the family unit (Chapais 2008), and even when applied to non-relatives, a high prosocial motivation may be beneficial if it sends a costly signal or serves to maintain one's good reputation (see below).

Capuchin monkeys may on the face of it not fit this picture. One could argue that the more stable group composition relative to chimpanzees, as well as increased paternity concentration and female philopatry (Fragaszy et al. 2004) could have led to more stable reciprocal relationships and higher average relatedness, thus favouring prosocial motivations. However, the same is true for most macaques, probably without increasing prosociality. Another explanation could be that capuchins also evolved higher prosocial motivations, because they, like many New World Monkeys, engage in allo-maternal care, such as infant carrying and regular food sharing from males to infants (ibid.). At the moment, no other convincing hypotheses exist for the taxonomic distribution of the components of prosociality among primates.

Finally, humans seem to have acquired a strong sensitivity to the (perceived) presence and size of an audience. There are two explanations for this. Firstly, the potentially high costs imposed on cheaters in a society of interdependent individuals (Boehm 1999; Gurven 2004; Kaplan et al. 2009; Marlowe 2009), which we have

internalized as "conscience", functioning to anticipate others' reactions (Trivers 1971; DeScioli and Kurzban 2009), have lead to an increase in prosocial behaviour in the presence of subtle cues of being watched. Secondly, individuals (mainly men) may send costly signals in the presence of large audiences, thus advertising themselves as valuable cooperation partners or mates (Smith and Bliege Bird 2005). This new sensitivity to being watched and to the size of the audience may lead to strong reactive prosociality, in the presence of subtle extrinsic stimuli (0'), or even to proactive prosociality, if the conscience effectively internalized the possibility that extrinsic stimuli are present (0). Finally, the recent rise of anonymous market societies with their need for larger-scale cooperation may have further modified psychology (Henrich et al. 2010).

In conclusion, we note that humans differ from their closest living relatives, the great apes, in two key aspects of the psychological regulation of cooperation: Humans are *proactive*, i.e. they act prosocial in the absence of obvious extrinsic stimuli and more *reactive*, i.e. they respond stronger to extrinsic stimuli and to a wider range of such stimuli. Thus, the parameters *a* (response to extrinsic stimuli) and *b* (intrinsic motivation) in Figure 4-1 differ between humans and great apes, indicating that prosociality has been under stronger positive selection during human evolution.

Chapter 5: Psychological altruism in non-human animals? Preconditions, an operational definition and the empirical evidence

Biological definitions of altruism (BA) are based on the *consequences* of actions as measured in costs and benefits to an actor's fitness. In contrast, philosophical views of altruism stress the *motives* of actions and include recognition of another person's desires and a genuine concern for those. However, since these proposed mental processes are often inaccessible, the empirical evidence for such psychological altruism (PA) remains controversial. We discuss the psychological preconditions for PA in animals, namely an understanding of the self and others as intentional agents, the ability to read others' intentions or desires and a motivation to satisfy them. Based on differences in these preconditions and the corresponding levels of intentionality we propose to distinguish between PA *sensu lato* and *sensu stricto* (which are, however, indistinguishable by observation) as well as non-intentional forms of BA. We suggest that a behavior is indicative of PA if *A* is an intentional agent, and changes its behavior in order to satisfy *B*'s goals as perceived by *A*, and if other immediate reasons such as harassment can be excluded. Using this definition, we review the empirical evidence for PA in various species, in particular in the contexts of food sharing and targeted helping. The disposition for PA of different species is compared with regard to the intensity, pervasiveness, extent and empathetic skill involved. Finally, we briefly discuss how natural selection for BA may have shaped these dispositions and why and to what extent humans differ from other animals.

This article is structured into six sections (I.-VI.). The first introduces the concepts of biological and psychological altruism (BA and PA) and notes that PA differs in that it refers to the motives and BA to the consequences of behaviors. In the second section we briefly discuss the difficulties of assessing an agent's "true" motives, which is why the presence of PA is so debated among humans. The third asks whether animals *could* have PA by identifying the necessary psychological requirements, namely some form of theory of mind and prosocial motivations, and by excluding other explanations for BA, in particular those that make PA so debated in humans. This section thus forms the core of the article and paves the way for the fourth section, which is concerned with how we could *recognize* PA in animals and presents an operational definition for doing so. In the fifth section we review empirical evidence to answer whether and to what extent animals *do have* PA as operationalized above. Finally, in the sixth section we briefly discuss *why* animals (including humans) should have PA, or in other words, under what conditions selection for BA should favor PA, thus linking the two again. Throughout the article we will mainly use the context of *food sharing* as a source of illustration but also discuss the evidence for other helping situations in part five.

I. What is altruism? Biological vs. psychological definitions

Several biologists have claimed that by understanding the evolution of altruism one can explain the evolution of morality (Wilson 1975; Alexander 1987; de Waal 2006). However, leaving aside the common objection of philosophers that morality is about more than just altruism (e.g. Peacock et al. 2005), the type of altruism that

biologists are typically concerned with is fundamentally different from philosophical (and indeed folk psychological) views of altruism, thus hampering any contribution of biologists to moral philosophy. In the following we briefly discuss these different views.

Biological altruism (BA)

Biologists defined altruism in terms of costs and benefits to Darwinian fitness, i.e. reproduction and survival (Hamilton 1964; Trivers 1971). Thus, BA is measured by the *consequences* of behavior. This approach has proven useful in explaining the evolution of altruism by ultimate mechanisms such as kin selection (Hamilton 1964) or reciprocal altruism (Trivers 1971), which aim to "take the altruism out of altruism" (ibid., p. 35), i.e. to show that behavior that is costly to the self but beneficial to another individual in the short term will still serve (genetic) self-interest in the long run. As we will argue in more detail below (Sections III. (iii), VI.), this long-term self interest is most probably not consciously represented by animals, and probably quite often also not by humans.

Even though Trivers (1971) devoted a large section of his paper on reciprocal altruism to its psychological regulation (in humans), the topic has been far less studied by biologists. Since many scholars who studied altruism worked on relatively simple organisms such as eusocial insects (e.g. Hamilton 1964; Wilson 1975), it was often assumed that the behavior was hard-wired, i.e. genetically predisposed to be triggered by specific stimuli. The question of psychological regulation arose only in the study of more complex organisms such as non-human primates (de Waal 1996; de Waal 2006). Since primates share with humans many aspects of social behavior it has been proposed

that they can help us to understand the origins of altruism in humans (ibid.). How then

is altruism defined by scholars of human behavior?

Psychological altruism (PA)

Generally speaking, psychologists and philosophers are concerned with the

motives and intentions of actions, not their consequences (e.g. Batson 1991). A very

concise definition of PA has been provided by Sober and Wilson (1998, p. 201) as "the

existence of ultimate[2] desires concerning the well-being of others". Or in the words of

Kitcher (1998, p. 284), "we think of people as altruists when they adjust their

preferences to their perceptions of the wants and needs of others". These definitions are

thus fundamentally different from BA.

Motives are also at the core of most important schools of moral philosophy.

Most famously, philosophers in the Hume-Smith tradition stress the importance of

moral emotions such as sympathy (Smith 2002 [1759]; Hume 2003 [1739-1740]) while

proponents of a new ethics of virtue invoke benevolence as a characteristic of human

"natural goodness" (Foot 2001). Kant (1994 [1785]) highlighted duty and reason and

postulated in his categorical imperative that another person was always to be treated as

an end in itself and never as a means to achieving some other end. Even early

consequentialists such as John Stuart Mill (1987 [1861]) recognized the importance of

altruistic motives. In general, when giving justifications for actions in moral discourse,

lay or academic, the motives of behavior often matter more than the consequences.

Thus, the kind of altruism "that matters to morality" (Kitcher 1998, p. 284) is PA and

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[2] Ultimate here indicates that the desires represent ends in themselves rather than means to achieving some other end (like increasing one's fitness). Thus, ultimate here is distinct from the biological meaning of the word.

not BA. Hence, if biologists wish to contribute to an understanding of altruism or morality as relevant to moral philosophers they should concern themselves with the motives underlying BA.

II. PA among humans: Inaccessibility of motives and skepticism

Before we consider animal altruism we have to mention one fundamental problem underlying the debate about psychological altruism in humans, namely the difficulty of distinguishing acts that only appear altruistic (in a BA sense) but are actually motivated by self-interest, from those that are genuinely altruistic, i.e. PA. Since the motives of actions are not directly accessible to outsiders, we have to rely on self reports by the actor or must try to infer the actor's motives from observation of his actions. Both these methods are flawed by inherent difficulties: First, an individual's motives may not be consciously experienced, as seen when *a posteriori* reasons are given for judgments actually made intuitively (Haidt 2001; Haidt 2007), and can thus also not be reliably reported. Furthermore, people tend to overemphasize their altruistic motives (Ridley 1996) and/or to deceive themselves about their own motives (Trivers 2010). Second, the problem with inferring motives from observation is that motives may "resist complete characterization in behavioural terms" (Peacock et al. 2005; p. 189), rendering unambiguous inferences impossible. Both these problems continue to fuel skepticism about PA in humans. But let us assume for the moment that humans at least occasionally engage in actions motivated by PA. How could we best recognize this from pure observation of their actions? This of course is the only available method for the study of *animal* altruism.

III. Could animals have PA? Preconditions and behavioral cues

The task of inferring motives from behavior may actually be somewhat less hopeless among animals, because animals are less likely than humans to pursue hidden egoistic goals when performing BA due to cognitive limitations (Kitcher 1985; Stevens and Hauser 2004; see discussion in III. (iii)). Thus, the risk of classifying behavior as PA that only appears to be altruistic, but is actually motivated by self-regard, is lower. However, for animals another main question is whether their actions are guided by anything like motives in a human sense, i.e. whether they recognize themselves and others as intentional agents.

For the purpose of discussing what preconditions animals must fulfill for their actions to be guided by motives and how PA can be inferred from observation of actions we will refer to an illustration of PA provided by Kitcher (1998, p. 284):

"There is some divisible good that is valued by both *A* and *B*; when *A* is alone and comes across this good, then *A* prefers taking it all to any other available option; however, if *A* recognizes that *B* is present (and, I assume, that *B* also values the good), then *A* no longer prefers consuming the good entire but, instead, wants most to share the good with *B*. Moreover, this preference is generated by *A*'s perception of *B*'s valuation of the good, and it is not explained by *A*'s having some other independent end that would be advanced by sharing with *B* – *A* does not calculate that, in the long run, more good things will accrue from sharing with *B*."

Now let us consider the relevant points in this illustration as emphasized by Kitcher (ibid.):

"First, *A*'s valuations differ between the solo situation and that in which *B* is present: it is not particularly unselfish for people to share things to which they attach no

value. Second, A's preference when *B* is present is mediated by the perception of *B*'s wants: [psychological] altruism presupposes an empathetic ability to discern what others need or desire and to respond to it. Third, *B*'s satisfaction is perceived as an end in itself, not as a means to the achievement of some of *A*'s other goals."

The first point (i) makes clear that *A* values the good when alone but *changes his valuation* in B's presence, the second (ii) states an "*empathetic ability*" as the generator of the altruistic motive and the third (iii) *excludes other motives*. If animals fulfill these psychological preconditions and if we can find behaviors that reliably indicate them, then an extension of PA to animals may be warranted.

(i) First, *A*'s valuation of the good when alone can easily be measured, especially if the good is food. The crucial point is that *A changes his valuation* in *B*'s presence. The only way to unequivocally identify a change in valuation is a *change in behavior*. For instance in a food sharing context, the fact that "*A* no longer prefers consuming the good entire" may be indicated when *A* stops or slows down his feeding in *B*'s presence, or even more so, if *A* actively makes food available *B* [3]. Hence, following Caro and Hauser (1992) in their operational definition for teaching, we will use a *change in behavior* as an indicator for a change in intention.

(ii) Second, this change in valuation, as indicated by a change in behavior, should be generated by an "*empathetic ability*", i.e. an ability to discern the other's needs or desires and to respond to them in an adequate way. Hence, some understanding of the other's internal state, i.e. some form of a *theory of mind* (ToM) is required, and it has to be coupled with a *prosocial motivation*, i.e. any internal mechanism that rewards

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[3] It may also be that *A* changes his valuation without changing his behavior, but there is no way for us to recognize that he/she did. For instance, if *A* does not actively make food available to *B*, but continues feeding in the same way and merely passively tolerates that *B* takes some food, there is no way of inferring whether *A* actually wanted *B* to have food. Thus, the operationalization is conservative in that it excludes potential cases of PA where there was no change in behavior despite a change in preference.

the self for other-regarding behavior and thus makes the actor respond to the other's need.

The evidence for or against ToM in non-human animals is still controversial (see e.g. Heyes 1998 and commentaries therein; Penn and Povinelli 2007). Arguably, the best evidence can be found in apes (Byrne 1995; Call and Tomasello 2008), although their ToM might be somewhat different from ours: For instance, Call and Tomasello (2008) concluded in a recent review that chimpanzees do understand others in terms of a perception-goal psychology, but do not possess a human-like belief-desire psychology[4]. Hence chimpanzees are probably the best candidates for having motives broadly resembling our own. Other animals have been far less systematically studied and the evidence is thus scarcer. We know from other great apes (Inoue-Nakamura 2001), dolphins (Reiss and Marino 2001), elephants (Plotnik et al. 2006), but also some birds (Prior et al. 2008) that they, like chimpanzees, can recognize themselves in a mirror, thus hinting at an understanding of the self (and presumably others) as intentional agents (Gallup and Platek 2002). We may thus assume that these species share a similar ToM with chimpanzees. No evidence for mirror self-recognition was found in monkeys (Heyes 1998; Heschl and Burkart 2006) but some species may have some recognition of others as intentional agents (e.g. Flombaum and Santos 2005; Burkart and Heschl 2007; Phillips et al. 2009). Finally, most other animals probably do not understand themselves and others as intentional agents and their behavior is assumed to be relatively hard-wired in terms of stimulus-response mechanisms.

These differences in ToM capacities correspond to differences in Dennett's (1983) levels of intentionality: in level 0, *A* simply responds to a *stimulus*, like birds do

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[4] There is as yet no standard experimental paradigm for testing belief-desire understanding in animals. An indication for it would be a rapid, adequate response in a novel situation, but the evidence for this remains largely anecdotal (Byrne 1995; Call & Tomasello 2008).

when feeding their chicks in response to their open beaks. Hence, there is no intention

underlying *A*'s behavior. In level 1, *A* responds to *B*'s *behavior*, for instance begging or

reaching for the food. Hence, *A* makes food available with the intention of satisfying *B*'s

behavioral goal. Finally, in level 2, *A* responds to *B*'s *internal state*, e.g. by recognizing

that *B* is hungry and desires food and hence provides food with the intention of

satisfying this desire. The problem is that in practice, level 1 and 2 are often

indistinguishable by observation (Byrne 1995)[5]. However, given that 2nd order

intentionality requires a belief-desire psychology for which there is little empirical

evidence in animals it is more parsimonious to assume 1st order intentionality in an

equivocal case.

Many may argue that only 2nd order intentionality, coupled with a full-blown

belief-desire ToM can correspond to human PA. However, very young children already

act out of empathic concern after they pass the age of mirror self-recognition, at roughly

18 months, but long before they develop a full-blown ToM, at around four years

(Eisenberg and Mussen 1989; Bischof-Köhler 1991; Koski and Sterck 2009). Hence, it

appears that agents who can recognize themselves in the mirror (and thus presumably

have a conception of themselves and others as intentional agents) and possess a

perception-goal psychology and 1st order intentionality may have motives for their

actions that are similarly relevant to PA as those with a belief-desire psychology and 2nd

order intentionality. Thus, we propose to distinguish between PA *sensu stricto*, probably

only present in adult humans and PA *sensu lato*, probably present in human children

and some species with mirror self-recognition and a perception-goal ToM (Table 5-1).

(In the following we will speak of a "well-developed ToM" to refer to either perception-

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[5] For instance, making food available in response to begging could be due to recognition of *B*'s goal of acquiring food or *B*'s need for food as inferred from the begging.

goal- or belief-desire psychology and of a "full-blown ToM" to refer only to the latter).
These two forms of PA have to be distinguished from BA that lacks intentionality, i.e.
biologically altruistic acts by animals that have no understanding of themselves or
others as intentional agents and the behavior of which is regulated by simple stimulus-
response mechanisms.

Table 5-1: Different levels of proximate regulation for biologically altruistic acts (BA), only some of which may count as psychologically altruistic (PA). Note that having a higher level of theory of mind (ToM) or intentionality alone is only a necessary but not sufficient precondition for PA, since the recognition of another agent's desires or goals is not _per se_ coupled with a desire to fulfill those, i.e. some prosocial motivation

Proximate regulation of BA	Level of ToM	Level of intentionality	Present in[a]
PA _sensu stricto_	Belief-desire psychology	2	Adult humans
PA _sensu lato_	Perception-goal psychology	1	Human children, great apes, probably dolphins, elephants, corvid birds, possibly some monkeys
Prosocial motivation without intention (hard-wired)	Stimulus-response	0	Rest of animal kingdom

Note that Kitcher's "empathetic ability" includes both the ability to discern the
other's need or desire as well as a motivation to respond to it. Hence, a well developed
ToM alone is only a necessary but not a sufficient condition for PA, since one can

perfectly well recognize another person's desires *without wanting to respond to them*[6].

Thus, ToM has to be coupled with some prosocial motivation, which does not arise

automatically from the recognition of the other's intentions or desires (Burkart et al.

2009). For instance, ToM among chimpanzees and birds is better developed in

competitive rather than cooperative situations (Hare and Tomasello 2004; Clayton et al.

2007), and thus most likely evolved in competitive contexts. On the other hand,

prosocial motivation alone, though not necessarily accompanied by ToM, is better

developed in other species, in particular those with a more cooperative natural history

(Jaeggi et al. in press).

(iii) To satisfy Kitcher's third criterion for PA, other motives for BA have to be

excluded, in particular those toward gaining indirect benefits to the actor. Those indirect

benefits can be either *immediate* (avoidance of harassment or coercion) or *delayed*

(through kin selection, reciprocity, reputation gain, etc.). Harassment can be observed

and thus altruistic acts as an avoidance of harassment can largely be excluded[7]. Pursuit

of delayed benefits cannot be measured. However, it is highly unlikely that animals

consciously pursue such benefits by calculating their genetic gains and losses or the

chances of future reciprocation due to obvious cognitive limitations (Kitcher 1985;

Stevens and Hauser 2004). Rather, the corresponding behavior is more parsimoniously

assumed to be emotionally regulated (Kitcher 1998; Wright 2006), following simple

rules-of-thumb (Jaeggi et al. in press).

For instance, consider a situation as discussed by Wright (2006) in which *A*

grooms *B* one day and *B* then helps *A* in a conflict the next day. As Wright pointed out,

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[6] See for example discussions of psychopaths, moral skeptics, rational fools etc. throughout the philosophical literature.
[7] An exception may be acting altruistically in *anticipation* of harassment, in which case altruistic acts from low-ranking to high-ranking individuals might have to be excluded, even if there was no overt harassment.

this can be explained both in terms of cognitive or emotional regulation: We can suppose that *A* knew about the imminent challenge and hence wanted to ensure *B*'s support by grooming *B*. *B*, having been groomed wanted to keep his part of the bargain (or was also pursuing some long-term egoistic goal) and thus supported *A*. Or, *A* felt insecurity because of recent challenges, and thus sought reassurance by grooming a valuable social partner *B* (it is well known that grooming reduces stress levels in both groomer and groomee). *B*, having been groomed, felt the bond with *A* strengthened and was thus more likely to support *A*. .Both explanations are possible in humans, but seeing that the former makes much stronger assumptions about the cognitive abilities of the actors (in terms of planning, memory, temporal discounting, etc., see Stevens and Hauser 2004), the latter is more parsimonious in non-human animals (Wright 2006). Furthermore, the respective brain areas indicate that emotional regulation is phylogenetically older (e.g. Panksepp 2004), and thus certainly preceded cognitive regulation in the primate lineage. Finally, several scholars have pointed out that altruistic behavior is *biologically* more successful if genuine, i.e. not serving consciously pursued goals, e.g. because this generates more trust, gratitude, etc., thus ensuring cooperation and maximizing the return-benefits from altruistic acts (e.g. Trivers 1971; Frank 1988; Kitcher 1998). Natural selection should thus have equipped agents with respective emotional dispositions rather than a full understanding of how those enhance their own fitness. Hence, if immediate reasons such as harassment or coercion can be ruled out, it is more parsimonious to assume that BA among animals is triggered by a prosocial motivation rather than by conscious pursuit of delayed benefits. Thus, *A* probably derives some internal satisfaction from aiding *B* and the act can thus

be seen as an end in itself. If *A* is an intentional agent, i.e. has a well-developed ToM (Table 5-1), we may infer PA.

In summary, some animals may fulfill the requirements for PA, at least in the broad sense defined here (Table 5-1). The next section provides an operational definition for inferring PA from observation.

IV. How to infer PA in animals: an operational definition

PA can be defined as adjusting one's preferences to one's perception of the wants and needs of others (Kitcher 1998). Following from the previous section, we propose that PA can be inferred by behavioral observation if the following criteria are fulfilled:

- *A* changes or adjusts its behavior in the presence of *B*

- *A*'s change in behavior aims at satisfying *B*'s goals as perceived by *A*

- *A* does so on a voluntary basis, i.e. unforced by *B*

The first point indicates that *A* changes its preferences or valuations, the second that this is intended to be beneficial for *B*, and the third that *A* does so voluntarily. For the first point, it may again be noted that a change in behavior is the only way to unequivocally infer a change in preferences or valuations, even if this could also be possible without a change in behavior. For the second point, the precondition is that *A* is an intentional agent, i.e. has some form of ToM, as known from other, independent contexts (Table 5-1). For the third point, it is assumed that the act is not performed out of a rational calculation of the delayed benefits that could accrue to *A*, , which is, as discussed above, unlikely to be the case among animals. Rather, an emotional regulation is assumed, i.e. *A* derives emotional satisfaction from aiding *B*.

Note that this definition is somewhat similar to Caro & Hauser's (1992) operational definition for teaching in non-human animals, in particular with regard to inferring intentions from behavior. They distinguished three types of teaching, only one of which ("active teaching") required the *intention* to teach, while the other two ("opportunity teaching" and "coaching") were merely consistent with the *function* of teaching. However, since PA is about intentions and not just function (which would be BA), the intention of the actor has to be an inherent part of the definition. Thus, just like active teaching was defined by the teacher's adjustment of behavior to the *perceived skill-level* of the pupil (Caro and Hauser 1992), PA has to be defined by the adjustment of behavior to the *perceived goals and intentions* of the recipient[8]. Hence the inherent importance of ToM.

V. Do animals have PA and to what extent? The empirical evidence

If the preconditions discussed in III are fulfilled, the operational definition may apply to all animal interactions that represent BA, i.e. those in which one individual incurs a cost and another benefits. The two main contexts which we discuss here are food sharing and targeted helping, because these most evidently represent BA Since the available literature is heavily biased towards non-human primates we mainly discuss this taxonomic group. We start by applying the operational definition to a food-sharing context, which is similar to the situation described by Kitcher (1998).

Food sharing, defined as the un-resisted transfer of food from *A* to *B*, is quite frequent among primates (Feistner and McGrew 1989; Brown et al. 2004), including

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[8] PA *sensu stricto* would require an adjustment of behavior to the perceived needs and desires of the recipient, but as noted above, this is indistinguishable from PA *sensu lato* by observation.

humans (Gurven 2004), and has often been used as a model for the evolution of "moral

building blocks" such as reciprocal obligations (de Waal 1989; de Waal 2006).

However, little attention has been paid to the underlying psychology, as inferred from

the ways in which food is actually transferred from *A* to *B* (Jaeggi et al. in press). The

operational definition of PA is fulfilled *only* when *A* changes its behavior, unforced by

B, in order to make food available for *B*. PA can thus be seen in active forms of sharing

(Figure 5-1). *A*'s failure to actively transfer food indicates a lack of PA (but see footnote

[4]), e.g. through passive forms of sharing, and of course even more so by resisting

transfers and not sharing at all. The most crucial element is that *A* performs some active

behavior, thus indicating a change in preferences. Ignoring *B* clearly does not so, even

when *B* is then allowed to take some food and the consequence of the interaction thus

also represents BA.

   Observations show that the vast majority of food sharing instances among

primates is of the latter kind (Figure 5-1), even among kin (transfer to infants). Note the

large differences to human children in similar experiments. In fact, even instances of

active sharing may reflect the intention to get rid of the beggar, even the own infant, by

giving bad food parts while withholding good food (e.g. Bard 1992; Ueno and

Matsuzawa 2004). Thus, PA is not commonly expressed in primate food sharing, at

least not in those species that possess the necessary "empathetic ability", i.e. a well

developed ToM to fulfill the criteria for PA *sensu lato*[9].

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[9] Note that some species that do share food more regularly, thus expressing stronger prosocial motivation, e.g. Callitrichids (Figure 1), may not require a ToM component to do so because it can always be assumed that others are food-motivated and the ToM load of the situation is thus so low that the behavior can be hard-wired. Food sharing among callitrichids then does not represent PA because they lack ToM, as evidenced by a lack of mirror self-recognition (Heschl & Burkart 2006).
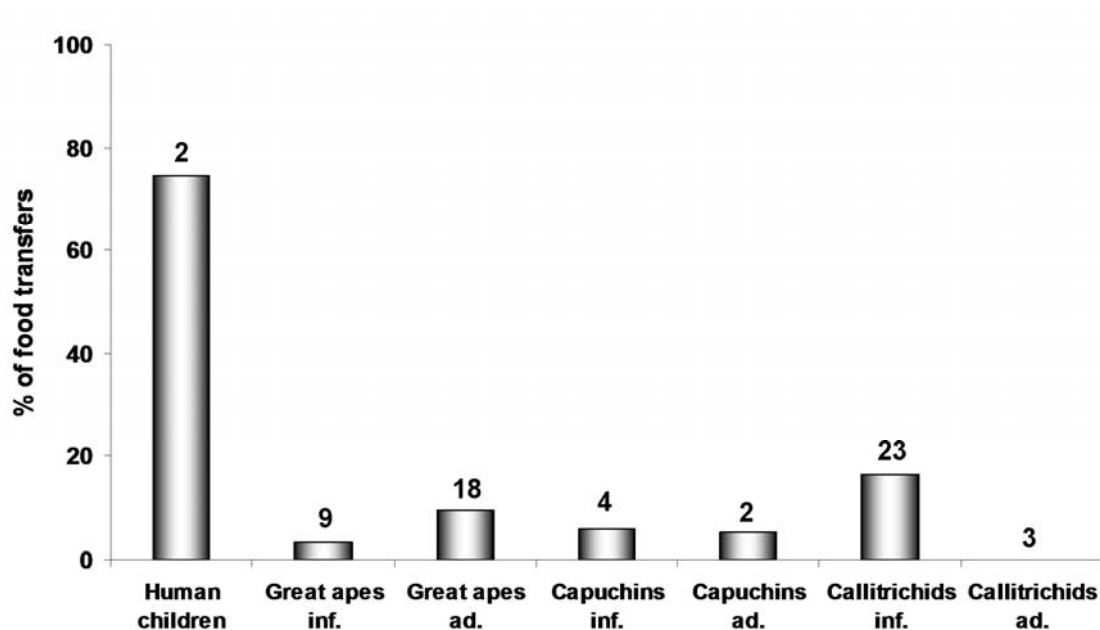
Figure 5-1: The proportion of un-resisted food transfers that were active, and thus may count as PA, in some of the best studies primate species. The numbers above the bars indicate the number of studies contributing to the means represented by the bars. Figure adapted from Jaeggi et al. (in press). inf. = transfers to infants, ad. = transfers among adults.

Furthermore, there are numerous instances where food owners fail to express PA by not taking others' goals into account, despite minimal costs. Consider the following situation from our own observations on bonobos[10]: *A* holds a large bundle of browse, such as the ones used by de Waal (1989), and allows *B* to feed from the same bundle (the situations thus representing BA). If *A* was a psychological altruist, he/she should take *B*'s position around the bundle into account, knowing that *B* wants to co-feed (and wanting *B* to be able to do so). However, food owners often turn their bundles about as they feed, forcing co-feeders to continuously adjust their position. Furthermore, if *A* is done feeding but the bundle still contains edible leaves and *B* is still co-feeding, *A*

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[10] Unpublished observations, for details on subjects see Jaeggi et al. (2010).

should hand over the bundle to *B* or at least make it easy for *B* to take the bundle. No substantial costs are involved with this action, and *A* can easily confer further benefits to *B*. However, in all instances we witnessed, food owners simply dropped their bundles when done feeding, making no effort whatsoever to facilitate *B*'s further feeding. Since they often sat high up in the enclosure, the former co-feeders had to climb down several meters to retrieve the bundle. In some cases this even led to scrambles or fights over ownership of the now deserted bundle. Surely, a psychological altruist would act differently. In fact, an actor *trying to maximize long-term self-interest* should also hand over the bundle rather than drop it, in order to increase delayed benefits through reciprocity or inclusive fitness. Thus, these observations also speak against a conscious representation of such egoistic goals.

Another context in which PA may be expressed is so-called *targeted or instrumental helping*. Defined as "helping that takes the specific needs of others into account" (de Waal 2003) it refers to situations in which an individual encounters some difficulty and another individual helps it to solve this difficulty by providing adequate help, e.g. by handing an object to an individual reaching for it, or opening a door for an individual trying to pass. Importantly, the "ToM-load" in targeted helping situations, can be considerably higher than in food sharing situations: Under naturalistic conditions, animals tend to be always food-motivated and it is thus not necessary to assess whether there is a desire for food or not in any new situation. Rather, the motivational state of food interest can be permanently built-in in a representation of con-specifics, either hardwired or by experience. Inferring the goals and intentions of others in targeted helping situations, however, is often not straight-forward and may require more sophisticated ToM capacities as well as an understanding of the relevant

physical constraints in the specific situation. Hence, BA in novel targeted helping situations cannot be hard-wired but requires the combination of prosocial motivation and ToM. Not surprisingly then, targeted helping is more common in species with well developed ToM such as great apes.

Targeted helping has been observed anecdotally (de Waal 2006) but has also been investigated experimentally with positive results for chimpanzees (Warneken and Tomasello 2006; Warneken et al. 2007; Yamamoto et al. 2009), bonobos (Hare and Kwetuenda 2010) and capuchin monkeys (Barnes et al. 2008). Thus, PA is expressed regularly in such paradigms. The most convincing evidence comes from the study on bonobos, in which subjects were alone in a cage with a large amount of food, which they would eat entirely when alone. However, when another individual was present in an adjacent cage, which the subject could open, most subjects stopped feeding quickly and opened the door to the adjacent cage, letting the other individual in to feed (Hare and Kwetuenda 2010). Thus, the subjects clearly changed their preferences in the presence of the other individual and acted in a way that satisfied the goals of the other individual as perceived by the subject. Note the differences to the bonobos observed by Jaeggi et al. (2010b).

Interestingly, in direct comparisons of human children and chimpanzees with varying degrees of enculturation, i.e. contact with humans, there seemed to be differences in PA (Warneken and Tomasello 2006; Warneken et al. 2007). In particular, the more enculturated the chimpanzees were, the higher their prosocial motivation seemed to be, probably because helping had been systematically rewarded by humans. For instance, *human-raised* chimpanzees spontaneously helped a human experimenter just like human children, suggesting that their prosocial motivation was similar

(Warneken and Tomasello 2006). In another comparison, *sanctuary-housed* chimpanzees responded slower than human children with helping and often only after solicitation by the experimenter, suggesting that their prosocial motivation may be lower (Warneken et al. 2007). Thus, chimpanzees may show PA in targeted helping situations, but do so more when they are well enculturated by humans (raising their prosocial motivation), and otherwise mainly upon request.

Overall, animals thus vary extensively in the four dimensions of PA defined by Kitcher (1998): intensity, pervasiveness, extent and empathetic skill. *Empathetic skill*, refers to the ability to identify the psychological dispositions of the recipient and is probably best developed in great apes with their perception-goal psychology (Call and Tomasello 2008) and possibly some other species (see Table 5-1, III. (ii)). The *intensity* of altruism, i.e. the degree of the altruist's movement away from his own (initial) desires is generally quite low among primates since most altruistic acts are of very low cost[11]. However, intensity may be higher in more cooperative species such as callitrichids who share food even more when it is preferred (Feistner and Chamove 1986) but may on the other hand lack an understanding of their own and others' intentions and desires and thus the ToM component of PA. Thus, callitrichids may give food calls to invite others to take food, indicating high prosocial motivation, but may experience conflict with their own desire to feed when others actually come to take food (own obs.). The *extent* of altruism is defined as the number of potential recipients, which for most animals is restricted to close kin and long-term bonded partners with whom there is a history of reciprocal interactions (cf. Burkart et al. 2009, Figure 1). Some argue that the same has been true for humans during the greater part of their

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[11] For instance, food is shared mainly after the owner is satiated and usually includes small scraps of food. Likewise, agonistic support is usually directed against subordinates where the risk of defeat or injury is minimal and grooming does not require much effort other than the time investment.

evolutionary history (Burnham and Johnson 2005), while others claim that it is precisely

an increase in the extent of altruism that made modern societies possible (Kitcher 1998;

Henrich et al. 2010). Finally, *pervasiveness* describes the range of contexts in which

altruism is expressed and among primates typically includes allo-grooming, agonistic

support, allo-maternal care and food sharing, all of which may not occur in every

species though.

Thus, in summary, many animals may show prosocial behavior, but only some

species do so coupled with a ToM component, i.e. an "empathetic ability" such that the

behavior could potentially qualify as PA. However, ToM in most non-human animals is

better expressed in competitive rather than cooperative contexts and thus probably

evolved in the former (Hare and Tomasello 2004; Clayton et al. 2007). Unless it is

coupled with prosocial motivation, ToM does not necessarily lead to PA. Among

chimpanzees in particular, enculturated individuals may show more PA than naturally

raised individuals, presumably because their prosocial motivation is higher due to the

frequent rewarding of such behavior by humans. .Hence, given the rareness of PA

among non-human animals, either because of a lack of ToM or a lack of prosocial

motivation, the question of the next section is how natural selection could have led to

PA.

VI. Conclusions: Why PA?

If BA does not need to be fine-tuned to the recipients desires, e.g. because these

can be assumed to be constant (need for food, shelter, grooming, predator avoidance

etc.), then such behavior can be regulated without ToM. Only in contexts where the

intentions of the recipient are not obvious there needs to be a coupling of prosocial

motivation and a ToM component, such as in targeted helping situations, thus leading to PA. However, those animals that do possess the cognitive preconditions for PA *sensu lato*, i.e. at least a perception-goal ToM, probably evolved these not in order to be altruistic but in order to compete better. Furthermore, no animals may be able to perform PA *sensu stricto* because they probably lack the necessary belief-desire psychology and 2nd order intentionality (Table 5-1). Hence, the interesting questions really are why humans evolved both a full-blown ToM and high prosocial motivations, combining both of them to perform PA (*sensu stricto*), and, why humans evolved the cognitive capacities to perform BA out of egoistic calculations, something which animals are probably not capable of and which has lead to the wide-spread skepticism about the genuineness of human PA.

The first question, why humans coupled a well-developed ToM with high prosocial motivation has been addressed by Burkart et al. (2009) who argued that the ToM components stem from the last common ancestor with chimpanzees (who evolved it in competitive contexts), while the high prosocial motivation is a derived feature shared with other highly cooperative species, but not with other apes. Thus, this coupling of ToM with high prosocial motivation led to its application in cooperative contexts and thus the systematic occurrence of targeted helping, i.e. PA (ibid., Figure 4). The evolution of a belief-desire ToM from a presumed perception-goal ToM in the last common ancestor with chimpanzees may also be explained by its application in more cooperative contexts (teaching, collective action, etc.) leading to the advent of shared intentionality, which facilitated further development of ToM (Tomasello and Carpenter 2007; Burkart et al. 2009).

However, a belief-desire psychology and 2nd order intentionality not only increased the capacity for PA but also for tactical deception (Byrne 1995), which leads us to the second question, why humans evolved the capacity for conscious regulation of altruistic acts. Since altruistic acts and the exchange thereof are much more frequent among humans than among chimpanzees (Jaeggi et al. in press), it is likely that there has been considerable selective pressure to evolve ever more sophisticated psychological mechanisms regulating altruistic acts, including deception and subtle cheating by mimicking genuine altruism (Trivers 1971). Thus, it is possible that "fake" altruism, not backed-up by genuine emotions, could be strategically used to pursue egoistic goals once the cognitive preconditions for doing so had been acquired. However, since the evolutionary arm's race between altruists and cheaters also led to well-developed detection mechanisms and countermeasures against subtle cheaters (ibid.), repeated successful use of strategic altruism is probably quite rare. Rather, "fake" altruists will soon face mistrust by others and eventually find themselves without any cooperation partners. Thus, we again emphasize that an emotional regulation of BA, i.e. PA, is functionally more successful because it ensures cooperation by building trust (Trivers 1971; Frank 1988) and genuine psychological altruists thus fare better in the long run. In other words, (most) humans are probably no rational fools (*sensu* Gauthier 1986), because the moral contract was made not by conscious agreement but by an emotional commitment to cooperation, i.e. PA, set in place by natural selection.

In summary, there are many instances of biologically altruistic behavior, only a few of which may represent psychological altruism in a philosophical sense, i.e. including an understanding of the intentions and goals of others as well as a genuine desire to advance these. This is partly due to the fact that few animal species possess the

necessary cognitive or motivational preconditions, possibly because the former evolved in more competitive contexts and are thus rarely coupled with the latter. Humans probably coupled the two components due to the adoption of a more cooperative lifestyle compared to the last common ancestor with other apes. Thus, if psychological altruism is taken as an important component of morality (Kitcher 1998; Sober and Wilson 1998), the interesting question for moral philosophers could be not whether humans do have psychological altruism or not, but under what conditions it was favored by natural selection, an understanding of which may help to advance its expression in modern societies.

Appendix

Chapter 1
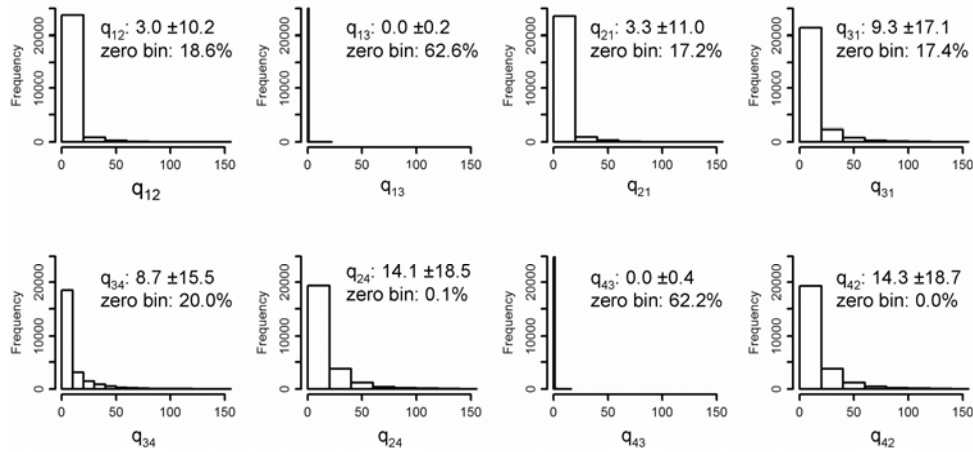
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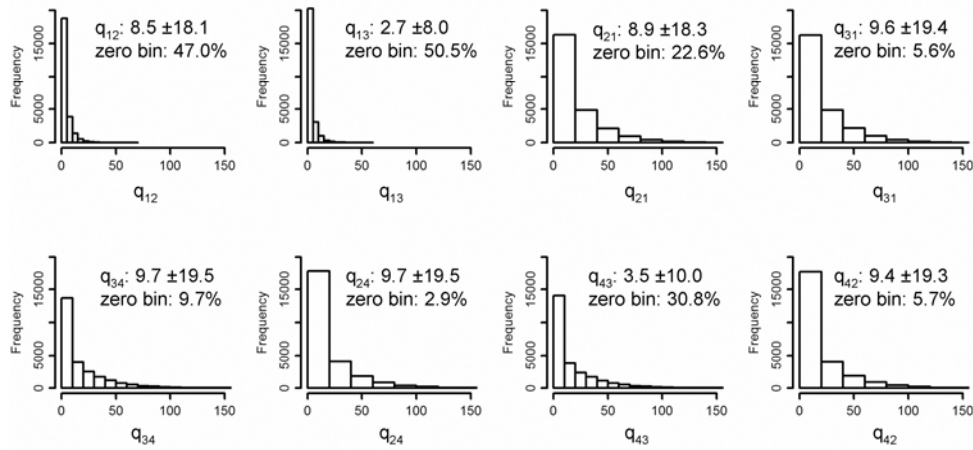
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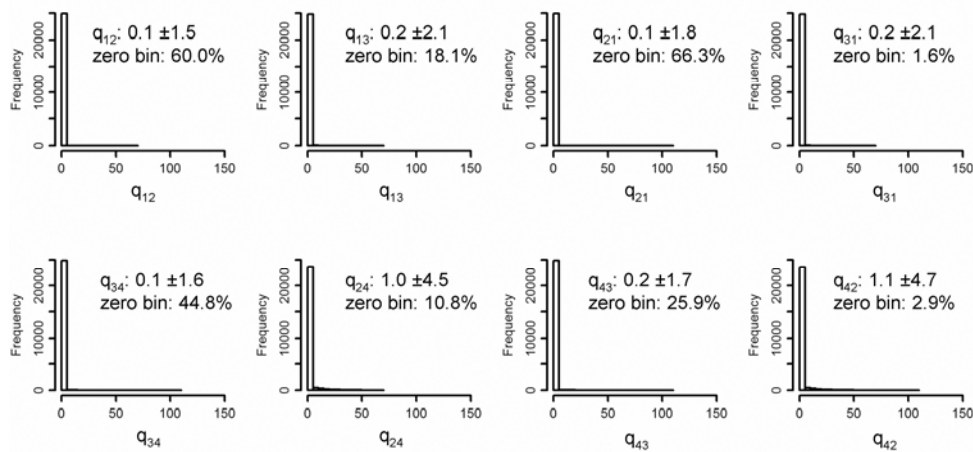
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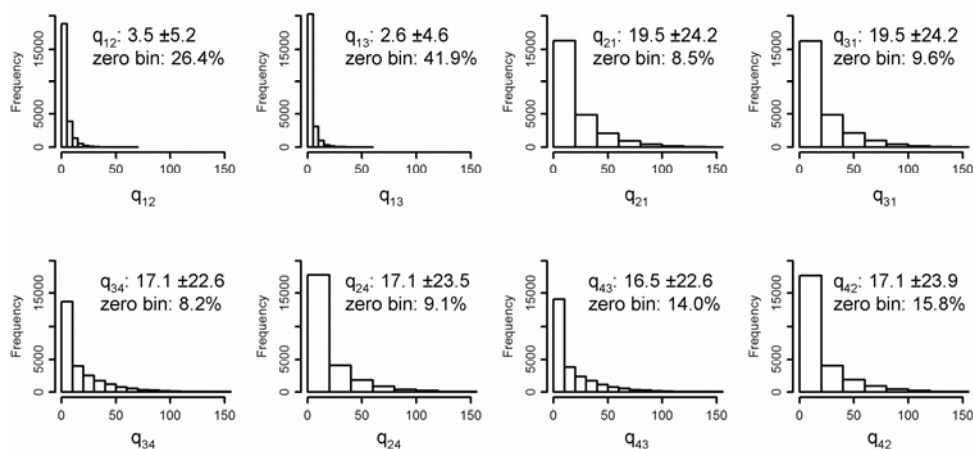
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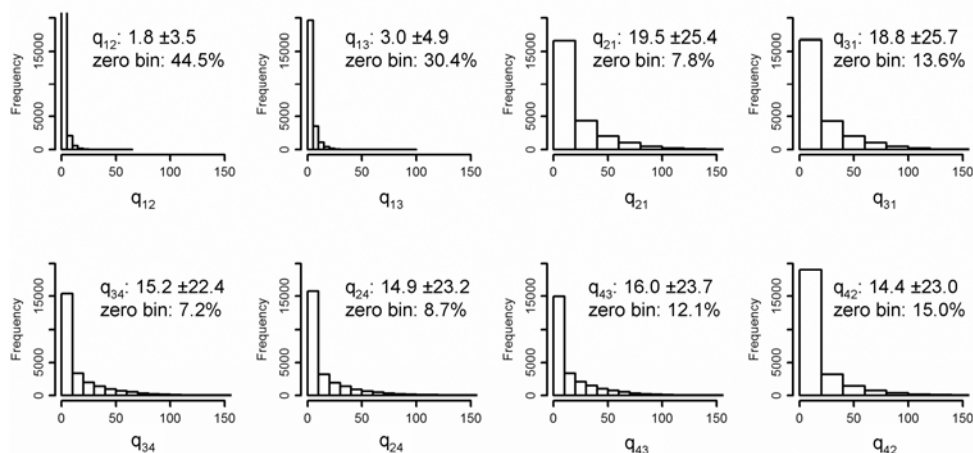
e)

Appendix 1-1: Following Pagel and Meade (2006), we plotted the posterior distributions of rate coefficients, i.e. estimated probabilities (*q*) for evolutionary transitions between states (see Figure 1-1). Rate pairs, i.e. the probabilities of gains or losses of one trait in the presence or absence of the other trait are arranged vertically. Differences between rate pairs provide evidence for correlated evolution, e.g. pairs q_{13} and q_{24}, which correspond to gains of food sharing with and without another trait of interest. The plots represent a) sharing among adults, sharing with infants, b) sharing from males to females, opportunity for female choice, c) sharing from males to females, monogamy, d) sharing among males, male-male coalitions, e) sharing among females, female-female coalitions. The written values are the mean ±SD values of *q* as well as the percentage of models that estimated *q* to zero ("zero bin")

Chapter 2

Appendix 2-1: Details on the composition of all (main and additional) study groups, individuals are

ranked according to age, arrows indicate offspring

Species	Group	Name	Date of Birth[1]	Sex	Included in[2]
Chimpanzees	Gossau	BL	1958	f	GS 1 & 2
		→ FA[3]	02/08/2000	f	GS 1 & 2
		NI	1976	f	GS 1 & 2
		→ DI	26/6/1992	m	GS 1 & 2
		CE	02/07/1976	m	GS 1 & 2
		BR	1981	f	GS 1 & 2
		CH	15/03/1984	f	GS 1 & 2
		→ TZ	02/08/1992	f	GS 1 & 2
		DA	01/12/1984	m	GS 1 & 2
		BA	24/08/1996	f	GS 1 & 2
		EL	19/03/1999	f	GS 1 & 2
	Gänserndorf a	SU	1974	f	GD a1 & 2
		LI	1981	f	GD a1 & 2
		AN	1982	m	GD a1 & 2
		BO	1982	f	GD a1 & 2
		HE	1982	f	GD a1 & 2
		→ AL	25/11/1996	m	GD a1 & 2
		SC	1982	f	GD a1 & 2
		→ DA	10/04/1998	m	GD a2
		→ XA	26/02/1999	f	GD a2
		MO	1983	m	GD a1 & 2
	Gänserndorf b	GO	1974	m	GD b
		IS	1978	m	GD b
		MA	1978	m	GD b
		JO	1981	m	GD b
		BL	1983	m	GD b
		JA	1983	m	GD b

|		MI	1985	m	GD b
Bonobos	Apenheul	MB	1980	m	A
		MW	1985	m	A
		ML	1985	f	A
		JI	15/07/1985	f	A
		RO	1990	f	A
		ZU	1990	f	A
		HA	1990	m	A
		LO	19/05/1992	f	A
	Planckendael	DE	1970	m	P 1 & 2
		DZ	1971	f	P 1 & 2
		→ LU	26/08/1994	m	P 1
		HE	1978	f	P 1 – 5
		HO	1978	f	P 1 – 5
		→ RE	24/11/1990	m	P 2 – 5
		→ VI	23/07/1994	m	P 3 - 4
		→ ZA	16/04/1998	m	P 4 - 5
		KO	1980	f	P 2
		KI	28/02/1983	m	P 1 – 5
		DJ	27/03/1995	f	P 3 – 5
	Twycross	DT	21/10/1977	f	T
		→ KC	19/04/1989	f	T
		→ KE	02/01/1994	m	T
		KA	07/06/1980	m	T
		BY	01/02/1990	f	T
		JS	02/08/1990	m	T
	Wuppertal	MT	22/12/1963	m	W
		LL	24/04/1980	f	W
		→ BD	17/09/1991	m	W
		LM	21/07/1980	m	W

BG	11/08/1989	m	W
EJ	14/07/1990	f	W

[1]dd/mm/yyyy, only estimated year is given if exact date is unknown
[2]Indicates in which study groups the individual was included (see Table 2-2)
[3]Arrows indicate offspring

Chapter 3
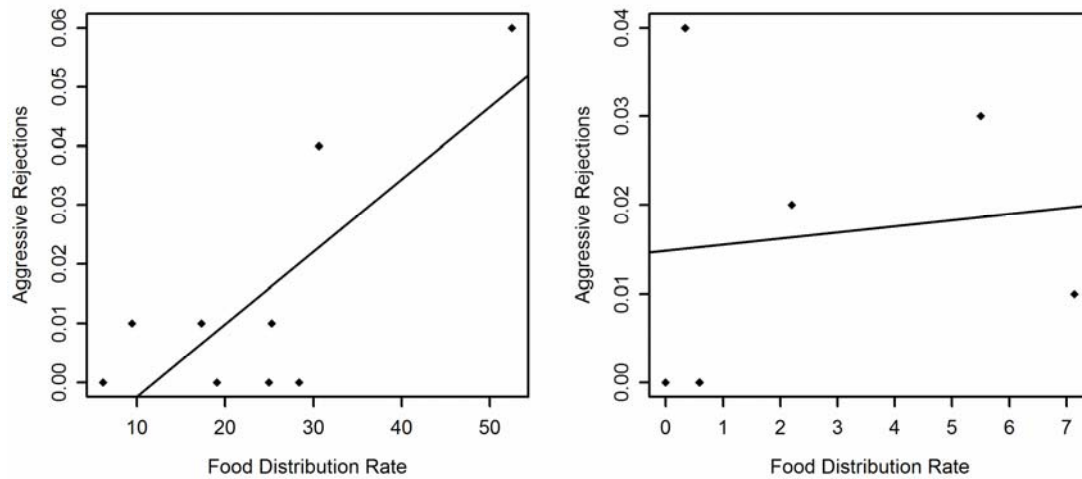
a)   b)

Appendix 3-1: The relationship between an individual's food distribution rate (transfers to others/h) and the amount of aggressive rejections received when approaching other food possessors for a) the chimpanzees and b) the bonobos. Averages over the whole study period were taken. The amounts of aggressive rejections were similar to the one reported by de Waal (1989) as was the food distribution rate of the chimpanzees. The food distribution rate of the bonobos was significantly lower (Wilcoxon: W = 195, P < 0.001). In contrast to de Waal (1989), neither group showed a negative correlation between food distribution rate and received aggressive rejections (Chimpanzees: Spearman's rho=0.51, N=9, P=0.16, Bonobos: rho= 0.2, N=6, P=0.7), hence no evidence for punishment was found
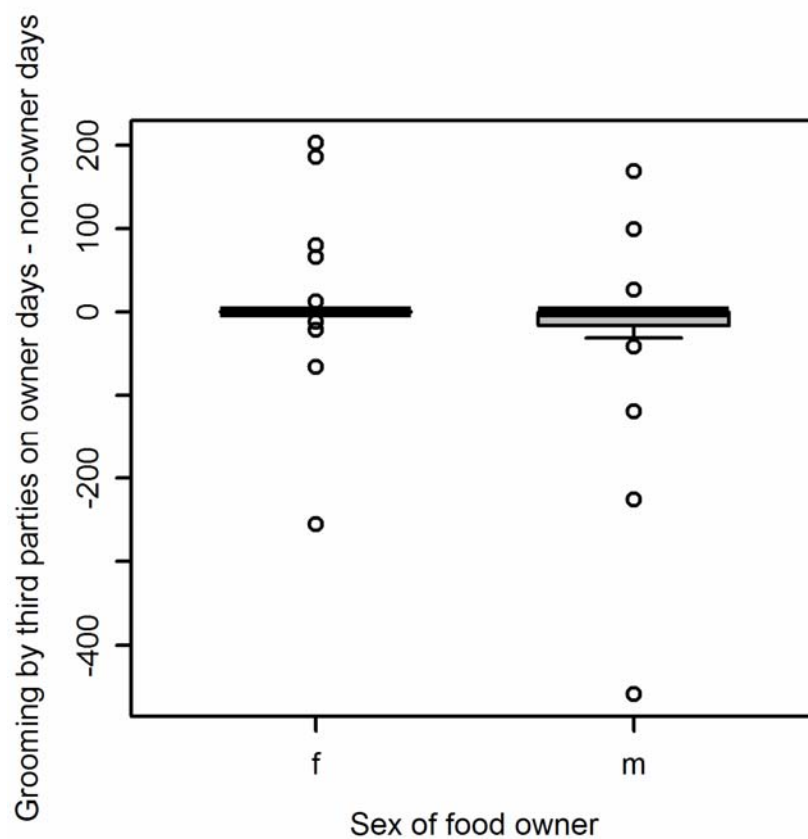
Appendix 3-2: The difference between grooming received (in seconds) by third parties after sharing sessions during which an individual was food owner compared to the closest sharing session during which it was not food owner, split by the sex of the food owner. There was no evidence that individuals were groomed more on days on which they were food owners (Wilcoxon: W=1208, P=0.79), thus not supporting the hypothesis that owning food per se makes individuals socially more attractive (Moore 1984)

Chapter 4

Appendix 4-1: Operational definitions of the food transfer types used

Term	Other terms	Operational definition	References
Proactive sharing (offering)		A *initiates* food transfer by calling B and may adopt a special "offering posture", or by approaching B, who was not begging, and allowing B to take food	(Brown and Mack 1978; Feistner and McGrew 1989; Gursky 2000; Wolovich et al. 2006)
Reactive sharing (active giving and facilitated taking upon begging)	Active sharing, active passive sharing	A *facilitates or aids* B's attempts to take food by making movements conducive to food transfer (includes actively handing over food as well as making it easier for B to take)	(Teleki 1973; Kuroda 1984; Boesch and Boesch 1989)
Passive sharing (tolerated taking)	Relaxed claim	A *tolerates* B's attempts to take food and neither discourages nor encourages them	(Teleki 1973; Boesch and Boesch 1989; de Waal 1989)

Appendix 4-2: Overview of all food sharing studies that presented detailed information on types of food transfers, allowing classification into *proactive*, *reactive* and *passive* sharing. The Table contains the species contributing to the means in Figure 4-1 (Callithrichids, capuchins, great apes and human children), as well as other primate species. Rows represent single studies or independent study groups and are ordered by species, in order of relatedness to humans

Sharing with infants

Group	Species	Environment	Pro-active	Re-active	Passive	Reference
Great apes	*Pongo pygmaeus*	wild	0	2.21	97.79	(Jaeggi et al. 2008)
Great apes	*Pongo pygmaeus*	free-ranging	0	16.19	83.81	(Bard 1992)
Great apes	*Gorilla gorilla*	wild	0	0	100	(Nowell and Fletcher 2006)
Great apes	*Pan paniscus*	wild	0	3.05	96.95	(Kuroda 1984)
Great apes	*Pan troglodytes*	captive	0	4.55	95.45	(Hirata and Celli 2003a)
Great apes	*Pan troglodytes*	captive	0	2.28	97.72	(Silk 1979)
Great apes	*Pan troglodytes*	wild	0	0	100	(McGrew 1975)
Great apes	*Pan troglodytes*	wild	0	0	100	(Lonsdorf 2006)
Great apes	*Pan troglodytes*	wild	0	0	100	(Silk 1978)
Gibbons	*Symphalangus syndactilus*	captive	0	0	100	(Fox 1972)
Gibbons	*Hylobates lar*	wild	0	0	100	(Nettelbeck 1998)
Gibbons	*Hylobates lar*	captive	0	0	100	(Schessler and Nash 1977)
Gibbons	*Nomascus concolor*	wild	0	0	100	(Fan and Jiang 2009)
Colobinae	*Procolobus badius temminckii*	wild	0	0	100	(Starin 2006)
Cercopithecinae	*Papio anubis*	wild	0	0	100	(Strum 1975; Strum 1981)
Capuchins	*Cebus capucinus*	wild	22.22	0	77.78	(Rose 1997)
Capuchins	*Cebus apella*	captive	0	0	100	(Fragaszy et al. 1997)
Capuchins	*Cebus apella*	captive	0	0	100	Furbush (cited in Fragaszy et al. 2004)
Capuchins	*Cebus apella*	captive	0	1	99	(Westergaard et al. 1999)
Callicebidae	*Callicebus torquatus*	wild	0	57.14	42.86	(Starin 1978)
Pitheciidae	*Pithecia pithecia*	wild	0	0	100	(Homburg 1997)
Callitrichids	*Leontopithecus rosalia*	captive	62.34	0	37.67	(Brown and Mack 1978)
Callitrichids	*Leontopithecus rosalia*	captive	5.96	0	94.04	(Price and Feistner 1993)
Callitrichids	*Leontopithecus rosalia*	wild	11.76	0	88.24	(Ruiz-Miranda et al. 1999)
Callitrichids	*Leontopithecus rosalia*	free-ranging	24.97	0	75.03	(Ruiz-Miranda et al. 1999)
Callitrichids	*Leontopithecus rosalia*	wild	19.24	0	80.76	(Rapaport and Ruiz-Miranda 2006)

Callitrichids	*Leontopithecus rosalia*	wild	18.15	0	81.84	(Rapaport and Ruiz-Miranda 2006)
Callitrichids	*Leontopithecus rosalia*	wild	37.25	0	62.75	(Rapaport and Ruiz-Miranda 2006)
Callitrichids	*Leontopithecus rosalia*	wild	5.65	0	94.35	(Rapaport 2006b)
Callitrichids	*Leontopithecus chrysomelas*	captive	20	0	80	Moura & Langguth, unpubl.
Callitrichids	*Leontopithecus chrysomelas*[a]	captive	5.80	0	94.20	(Feistner and Price 1999)
Callitrichids	*Leontopithecus chrysopygus*	captive	5.3	0	94.7	(Feistner and Price 2000)
Callitrichids	*Saguinus oedipus*	captive	48.65	0	51.35	(Feistner and Price 1999)
Callitrichids	*Saguinus oedipus*	captive	37.4	0	62.6	(Feistner and Price 1990)
Callitrichids	*Saguinus oedipus*	captive	35.4	0	64.6	(Feistner and Price 1990)
Callitrichids	*Saguinus oedipus*	captive	29.8	0	30.6	(Feistner and Price 1990)
Callitrichids	*Saguinus oedipus*	captive	9	0	91	(Feistner and Price 1990)
Callitrichids	*Saguinus oedipus*	captive	0	0	100	(Roush and Snowdon 2001)
Callitrichids	*Saguinus bicolor*	captive	1.5	0	98.5	(Price and Feistner 2001)
Callitrichids	*Saguinus labiatus*	captive	0	0	100	(Caine et al. 1995)
Callitrichids	*Saguinus mystax*	wild	0	0	100	(Heymann 1996)
Callitrichids	*Callithrix jacchus*	captive	0	0	100	(Feistner and Price 1991)
Callitrichids	*Callithrix geoffreoyi*	captive	0	0	100	(Feistner and Price 1991)
Callitrichids	*Callithrix argentata*	captive	0	0	100	(Feistner and Price 1991)
Tarsiidae	*Tarsius spectrum*	wild	27.78	0	72.22	(Gursky 2000)

Sharing among adults

Human children	*Homo sapiens*	pre-schools	16.86	64.17	18.97	(Birch and Billman 1986)
Human children	*Homo sapiens*	pre-schools	27.08	41.35	31.57	(Rao and Stewart 1999)
Great apes	*Pongo spp.*	wild	0	0	100	(van Noordwijk and van Schaik 2009)
Great apes	*Pan paniscus*	wild	0.67	12.34	86.96	(Kuroda 1984)
Great apes	*Pan paniscus*	wild	0	34	66	(Fruth and Hohmann 2002)
Great apes	*Pan paniscus*	captive	0	0	100	(de Waal 1992)
Great apes	*Pan paniscus*	captive	0	0	100	(Jaeggi et al. 2010b)
Great apes	*Pan troglodytes*	captive	0	0	100	(de Waal 1997)
Great apes	*Pan troglodytes*	captive	0	0.2	99.8	(de Waal 1989)
Great apes	*Pan troglodytes*	wild	0	1.34	98.65	(Teleki 1973)
Great apes	*Pan troglodytes*	wild	0	0	100	(Hockings et al. 2007)

Great apes	*Pan troglodytes*	captive	1.02	27.55	71.43	(Jaeggi et al. 2010b)
Great apes	*Pan troglodytes*	wild	0	30.77	69.23	(Nishida 1970)
Great apes	*Pan troglodytes*	wild	0	0	100	(Takahata et al. 1984)
Great apes	*Pan troglodytes*	wild	0	0	100	(Kawanaka 1982)
Great apes	*Pan troglodytes*	wild	0	0	100	(Nakamura and Itoh 2001)
Great apes	*Pan troglodytes*	wild	0	7.63	92.37	(Boesch and Boesch 1989)
Great apes	*Pan troglodytes*	wild	0	0	100	(Nishida et al. 1979)
Great apes	*Pan troglodytes*	wild	22.22	33.33	44.44	(Reynolds 2005)
Great apes	*Pan troglodytes*	wild	0	0	100	(Kuroda et al. 1996)
Gibbons	*Hylobates lar*	captive	0	0	100	(Berkson and Schusterman 1964)
Gibbons	*Nomascus concolor*	wild	0	0	100	(Fan and Jiang 2009)
Callitrichids	*Saguinus nigricollis*	wild	0	0	100	(Izawa 1978)
Colobinae	*Procolobus badius temminckii*	wild	0	0	100	(Starin 2006)
Colobinae	*Rhinopithecus roxellana*	captive	0	0	100	(Zhang et al. 2008)
Cercopithecinae	*Papio anubis*	wild	0	0	100	(Strum 1975; Strum 1981)
Capuchins	*Cebus apella*	captive	0	10.32	89.64	(de Waal et al. 1993)
Capuchins	*Cebus capucinus*	wild	0	0	100	(Rose 1997)
Aotidae	*Aotus azarai*	captive	4.65	0	95.35	(Wolovich et al. 2006)
Callitrichids	*Callithrix flaviceps*	wild	0	0	100	(Ferrari 1992)
Callitrichids	*Callithrix jacchus*	captive	0	0	100	(Kasper et al. 2008)
Callitrichids	*Saguinus nigricollis*	wild	0	0	100	(Izawa 1978)

[a]sharing with infant of different species (*Saguinus oedipus*)

Bibliography

Alexander RD (1987) The biology of moral systems. Aldine de Gruyter, New York

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour
49:227-267

Aureli F, de Waal FBM (1997) Inhibition of social behavior in chimpanzees under high-
density conditions. American Journal of Primatology 41:213-228

Aureli F, Schaffner CM, Verpooten J, Slater K, Ramos-Fernandez G (2006) Raiding
parties of male spider monkeys: Insights into human warfare? American Journal
of Physical Anthropology 131:486-497

Baayen RH (2009) languageR: Data sets and functions with "Analyzing linguistic data:
A practical introduction to statistics". In, 0.955 edn

Badrian A, Badrian N (1984) Social organization of *Pan paniscus* in the Lomako
Forest, Zaire. In: Susman RL (ed) The pygmy chimpanzee: evolutionary biology
and behavior. Plenum Press, New York, pp 325-346

Badrian N, Malenky RK (1984) Feeding ecology of *Pan paniscus* in the Lomako Forest,
Zaire. In: Susman RL (ed) The pygmy chimpanzee: evolutionary biology and
behavior. Plenum Press, New York, pp 275-299

Baldwin JD, Baldwin JI (1973) Interactions between adult female and infant howling
monkeys (*Alouatta palliata*). Folia Primatologica 20:27-71

Bard KA (1987) Behavioral development in young orangutans: Ontogeny of object
manipulation, arboreal behavior, and food sharing. PhD Thesis. In. Georgia
State University, Atlanta

Bard KA (1992) Intentional behavior and intentional communication in young free-ranging orangutans. Child Development 63:1186-1197

Bardsley N (2008) Dictator game giving: altruism or artefact? Experimental Economics 11:122-133

Barnes JL, Hill T, Langer M, Martinez M, Santos LR (2008) Helping behaviour and regard for others in capuchin monkeys (*Cebus apella*). Biology Letters 4:638-640

Barrett L, Henzi P, Rendall D (2007) Social brains, simple minds: does social complexity really require cognitive complexity? Philosophical Transactions of the Royal Society B-Biological Sciences 362:561-575

Bates D, Maechler M (2009) lme4: Linear mixed-effects models using S4 classes. In, 0.999375-31 edn

Bates D, Maechler M (2010) lme4: Linear mixed-effects models using S4 classes. In, 0.999375-33 edn

Bateson M, Nettle D, Roberts G (2006) Cues of being watched enhance cooperation in a real-world setting. Biology Letters 2:412-14

Batson CD (1991) The altruism question: towards a psychological answer. Lawrence Erlbaum Associates, Hillsdale

Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM (2003) Hierarchical classification by rank and kinship in baboons. Science 302:1234-1236

Berkson G, Schusterman RJ (1964) Reciprocal food sharing of gibbons. Primates 5:1-10

Bertrand M (1969) Behavioral repertoire of stumptail macaque - a descriptive and comparative study. Bibliotheca Primatologica 11:1-273

Bethell E, Whiten A, Muhumuza G, Kakura J (2000) Active plant food division and

    sharing by wild chimpanzees. Primate Report 56:67-71

Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R,

    Price SA, Vos RA, Gittleman JL, Purvis A (2007) The delayed rise of present-

    day mammals. Nature 446:507-512

Birch LL, Billman J (1986) Preschool childrens food sharing with friends and

    acquaintances. Child Development 57:387-395

Bischof-Köhler D (1991) The development of empathy in children. In: Lamb ME,

    Keller H (eds) Infant development. Lawrence Erlbaum, Hillsdale NJ, pp 245-

    275

Blurton Jones NG (1984) A selfish origin for human food sharing - tolerated theft.

    Ethology and Sociobiology 5:1-3

Boehm C (1999) Hierarchy in the forest: The evolution of egalitarian behavior. Harvard

    University Press, Cambridge, MA

Boesch C (1994) Cooperative hunting in wild chimpanzees. Animal Behaviour 48:653-

    667

Boesch C (2007) What makes us human (*Homo sapiens*)? The challenge of cognitive

    cross-species comparison. Journal of Comparative Psychology 121:227-240

Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Taï forest:

    Behavioural ecology and evolution. Oxford Univ Press, Oxford

Boesch C, Boesch H (1989) Hunting behavior of wild chimpanzees in the Taï National

    Park. American Journal of Physical Anthropology 78:547-573

Boesch C, Bolé C, Eckhardt N, Boesch H (2010) Altruism in forest chimpanzees: The

    case of adoption. PLoS ONE 5:e8901

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127-135

Bowler M, Bodmer M (2009) Social behavior in fission-fusion groups of red uakari monkeys (*Cacajao calvus ucayalii*). American Journal of Primatology 71:976-987

Brandon-Jones D, Eudey AA, Geissmann T, Groves CP, Melnick DJ, Morales JC, Shekelle M, Stewart CB (2004) Asian primate classification. International Journal of Primatology 25:97-164

Brosnan SF, Beran MJ (2009) Trading behavior between conspecifics in chimpanzees, *Pan troglodytes*. Journal of Comparative Psychology 123:181-194

Brosnan SF, Bshary R (in press) Defining cooperation and cheating. Philosophical Transactions of the Royal Society B-Biological Sciences

Brosnan SF, de Waal FBM (2002) A proximate perspective on reciprocal altruism. Human Nature 13:129-152

Brosnan SF, de Waal FBM (2009) *Cebus apella* tolerate intermittent unreliability in human experimenters. International Journal of Primatology 30:663-674

Brosnan SF, Silk JB, Henrich J, Mareno MC, Lambeth SP, Schapiro SJ (2009) Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. Animal Cognition 12:587-597

Brotherton PNM, Clutton-Brock TH, O'Riain MJ, Gaynor D, Sharpe L, Kansky R, McIlrath GM (2001) Offspring food allocation by parents and helpers in a cooperative mammal. Behavioral Ecology 12:590-599

Brown GR, Almond REA, Bates NJ (2005) Adult-infant food transfer in common

marmosets: An experimental study. American Journal of Primatology 65:301-

312

Brown GR, Almond REA, Van Bergen Y (2004) Begging, stealing, and offering: Food

transfer in nonhuman primates. Advances in the Study of Behavior 34:265-295

Brown K, Mack DS (1978) Food sharing among captive *Leontopithecus rosalia*. Folia

Primatologica 29:268-290

Brownell CA, Svetlova M, Nichols S (2009) To share or not to share: When do toddlers

respond to another's needs? Infancy 14:117-130

Bshary R, Grutter AS (2006) Image scoring and cooperation in a cleaner fish

mutualism. Nature 441:975-978

Burkart JM, Fehr E, Efferson C, van Schaik CP (2007) Other-regarding preferences in a

non-human primate: Common marmosets provision food altruistically.

Proceedings of the National Academy of Sciences of the United States of

America 104:19762-19766

Burkart JM, Heschl A (2007) Understanding visual access in common marmosets,

Callithrix jacchus: perspective taking or behaviour reading? Animal Behaviour

73:457-469

Burkart JM, Hrdy SB, van Schaik CP (2009) Cooperative breeding and human

cognitive evolution. Evolutionary Anthropology 18:175-186

Burkart JM, van Schaik CP (2010) Cognitive consequences of cooperative breeding in

primates? Animal Cognition 13:1-19

Burnham T, Hare B (2007) Engineering human cooperation. Human Nature 18:88-108

Burnham TC, Johnson DDP (2005) The biological and evolutionary logic of human

cooperation. Analyse & Kritik 27:113-135

Byrne RW (1995) The thinking ape: Evolutionary origins of intelligence. Oxford Univ

Press, Oxford

Caine NG, Addington RL, Windfelder TL (1995) Factors affecting the rates of food

calls given by red-bellied tamarins. Animal Behaviour 50:53-60

Caldwell CA, Whiten A (2003) Scrounging facilitates social learning in common

marmosets, *Callithrix jacchus*. Animal Behaviour 65:1085-1092

Call J, Tomasello M (2008) Does the chimpanzee have a theory of mind? 30 years later.

Trends in Cognitive Sciences 12:187-192

Camerer C (2003) Behavioral game theory. Princeton University Press, Princeton

Carlsen F (2007) European studbook for the chimpanzee *Pan troglodytes*. In,

Copenhagen Zoo, Denmark

Caro TM, Hauser MD (1992) Is there teaching in nonhuman animals? Quarterly Review

of Biology 67:151-74

Carpenter C (1940) A field study in Siam of the behavior and social relations of the

gibbon (*Hylobates lar*). Comparative Psychology Monographs 16:1-212

Carpenter CR (1934) A field study of the behavior and social relations of howling

monkeys (*Alouatta palliata*). Comparative Psychology Monographs 10:1-168

Carpenter CR (1965) The howlers of Barro Colorado Island. In: DeVore I (ed) Primate

behavior. Field studies of monkey and apes. Holt, Rinehart and Winston, New

York, pp 250-291

Carroll JB (1978) The maintenace and breeding of the silvery marmoset *Callithrix*

argentata at the Jersey Zoological park. Le Dodo 15:41-45

Cebul MS, Epple G (1984) Father-offspring relationships in laboratory families of

saddle-back tamarins (*Saguinus fuscicollis*). In: Taub DM (ed) Primate

paternalism. Van Nostrand Reinhold Company, New York, pp 1-19

Chalmers NR, Lockehaydon J (1984) Correlations among measures of playfulness and

skillfulness in captive common marmosets (*Callithrix jacchus jacchus*).

Developmental Psychobiology 17:191-208

Chapais B (2006) Kinship, competence and cooperation in primates. In: Kappeler PM,

van Schaik CP (eds) Cooperation in primates and humans. Springer, Berlin

Chapais B (2008) Primeval kinship: How pair-bonding gave birth to human society.

Harvard Univ Press, Cambridge, MA

Christen A (1968) Care and breeding biology of *Cebuella*. Folia Primatologica 8:41-49

Clayton NS, Dally JM, Emery NJ (2007) Social cognition by food-caching corvids. The

western scrub-jay as a natural psychologist. Philosophical Transactions of the

Royal Society B-Biological Sciences 362:507-522

Cleveland J, Snowdon CT (1984) Social development during the first 20 weeks in the

cotton-top tamarin (*Saguinus oedipus*). Animal Behaviour 32:432-444

Clutton-Brock TH (2002) Breeding together: Kin selection and mutualism in

cooperative vertebrates. Science 296:69-72

Clutton-Brock TH (2009) Cooperation between non-kin in animal societies. Nature

462:51-57

Clutton-Brock TH, Brotherton PNM, O'Riain MJ, Griffin AS, Gaynor D, Kansky R,

Sharpe L, McIlrath GM (2001) Contributions to cooperative rearing in meerkats.

Animal Behaviour 61:705-710

Clutton-Brock TH, Parker GA (1995) Punishment in animal societies. Nature 373:209-
216

Colman AD, Liebold KE, Boren JJ (1969) A method for studying altruism in monkeys.
The Psychological Record 19:401-405

Crockford C, Wittig RM, Seyfarth RM, Cheney DL (2007) Baboons eavesdrop to
deduce mating opportunities. Animal Behaviour 73:885-890

Cronin KA, Schroeder KKE, Rothewell ES, Silk JB, Snowdon CT (2009) Cooperatively
breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their
long-term mates. Journal of Comparative Psychology 123:231-241

Cronin KA, Snowdon CT (2008) The effects of unequal reward distributions on
cooperative problem solving by cottontop tamarins, *Saguinus oedipus*. Animal
Behaviour 75:245-257

Dare R (1974) Food-sharing in free-ranging *Ateles geoffroyi* (red spider monkeys).
Laboratory Primate Newsletter 13:19-21

Darwin C (1859 [1985]) On the origin of species by means of natural selection.
Penguin, London

Darwin C (1982 [1871]) The descent of man, and selection in relation to sex. Princeton
University Press, Princeton

Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

de Lyra-Neves RM, Oliveira MAB, Telino-Junior WR, dos Santos EM (2007)
Interspecific behaviour between *Callithrix jacchus* (Linnaeus) (Callitrichidae,
Primates) and some birds of the Atlantic forest, Pernambuco state, Brazil.
Revista Brasileira de Zoologia 24:709-716

de Vries H (1993) The rowwise correlation between two proximity matrices and the partial rowwise correlation. Psychometrika 58:53-69

de Vries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Animal Behaviour 50:1375-1389

de Vries H, Netto WJ, Hanegraaf PLH (1993) Matman - a program for the analysis of sociometric matrices and behavioral transition matrices. Behaviour 125:157-175

de Vries H, Stevens JMG, Vervaecke H (2006) Measuring and testing the steepness of dominance hierarchies. Animal Behaviour 71:585-592

de Waal FBM (1982) Chimpanzee politics: Power and sex among apes. Jonathan Cape, London

de Waal FBM (1989) Food sharing and reciprocal obligations among chimpanzees. Journal of Human Evolution 18:433-459

de Waal FBM (1991) Complementary methods and convergent evidence in the study of primate social cognition. Behaviour 118:297-320

de Waal FBM (1992) Appeasement, celebration, and food sharing in the two *Pan* species. In: Nishida T, McGrew WC, Marler P, Pickford M, De Waal FBM (eds) Topics in primatology. Volume 1: Human origins. University of Tokyo Press, Tokyo, pp 37-50

de Waal FBM (1996) Good natured: The origin of right and wrong in humans and other animals. Harvard Univ Press, Cambridge

de Waal FBM (1997) The chimpanzee's service economy: Food for grooming. Evolution And Human Behavior 18:375-386

de Waal FBM (2000) Attitudinal reciprocity in food sharing among brown capuchin monkeys. Animal Behaviour 60:253-261

de Waal FBM (2003) On the possibility of animal empathy. In: Manstead T, Frijda N,

    Fischer A (eds) Feelings and emotions: The Amsterdam symposium. Camrbidge

    Univ Press, Cambridge, pp 379-399

de Waal FBM (2005) Our inner ape: The best and worst of human nature. Riverhead,

    New York

de Waal FBM (2006) Primates and philosophers. How morality evolved. Princeton

    University Press, Princeton NJ

de Waal FBM, Berger ML (2000) Payment for labour in monkeys: capuchins will

    voluntarily share treats with other monkeys that helped to secure them. Nature

    404:563

de Waal FBM, Lanting FL (1997) Bonobo, the forgotten ape. University of California

    Press, Berkeley and Los Angeles

de Waal FBM, Leimgruber K, Greenberg AR (2008) Giving is self-rewarding for

    monkeys. Proceedings of the National Academy of Sciences of the United States

    of America 105:13685-13689

de Waal FBM, Luttrell LM, Canfield ME (1993) Preliminary data on voluntary food

    sharing in brown capuchin monkeys. American Journal of Primatology 29:73-78

de Waal FBM, Suchak M (in press) Motivation and cognition behind primate

    cooperation and deception. Philosophical Transactions of the Royal Society B-

    Biological Sciences

Dennett DC (1983) Intentional systems in cognitive ethology - the Panglossian

    paradigm defended. Behavioral and Brain Sciences 6:343-355

DeScioli P, Kurzban R (2009) Mysteries of morality. Cognition 112:281-299

Dufour V, Pele M, Neumann M, Thierry B, Call J (2009) Calculated reciprocity after all: computation behind token transfers in orang-utans. Biology Letters 5:172-175

Dunbar RIM (2004) Gossip in evolutionary perspective. Review of General Psychology 8:100-110

Dunbar RIM (2010) The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. Neuroscience & Biobehavioral Reviews 34:260-268

Earley R (in press) How communication networks affect cooperation and deception. Philosophical Transactions of the Royal Society B-Biological Sciences

Eisenberg N, Mussen PH (1989) The roots of prosocial behavior in children. Cambridge University Press, Cambridge

Ellefson JO (1968) Territorial behavior in the common white-handed gibbon, *Hylobates lar* Linnaeus. In: Jay PC (ed) Primates: Studies in adaptation and variability. Holt, Rinehart and Winston, New York, pp 180-199

Epple G (1967) Vergleichende Untersuchungen über Sexual- und Sozialverhalten der Krallenaffen (*Hapalidae*). Folia Primatologica 7:37-65

Fan P-f, Jiang X-l (2009) Predation on giant flying squirrels (*Petaurista philippensis*) by black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Yunnan, China. Primates 50:45-49

Faraway JJ (2006) Extending the linear model with R. Chapman & Hall, London

Fehr E, Bernhard H, Rockenbach B (2008) Egalitarianism in young children. Nature 454:1079-1083

Fehr E, Fischbacher U (2003) The nature of human altruism. Nature 425:785-791

Fehr E, Gachter S (2002) Altruistic punishment in humans. Nature 415:137-140

Fehr E, Schneider F (2010) Eyes are on us, but nobody cares: are eye cues relevant for
    strong reciprocity? Proceedings of the Royal Society B - Biological Sciences
    277:1315-1323

Feistner ATC, Ashbourne CJ (1994) Infant development in a captive-bred aye-aye
    (*Daubentonia madagascariensis*) over the first year of life. Folia Primatologica
    62:74-92

Feistner ATC, Chamove AS (1986) High motivation toward food increases food-
    sharing in cotton-top tamarins. Developmental Psychobiology 19:439-52

Feistner ATC, McGrew WC (1989) Food-sharing in primates: A critical review. In:
    Seth PK, Seth S (eds) Perspectives in primate biology. Volume 3. Today and
    Tomorrow's Printers and Publishers, New Delhi, India, pp 21-36

Feistner ATC, Price EC (1990) Food sharing in cotton-top tamarins (*Saguinus oedipus*).
    Folia Primatologica 54:34-45

Feistner ATC, Price EC (1991) Food offering in new-world primates - 2 species added.
    Folia Primatologica 57:165-168

Feistner ATC, Price EC (1999) Cross-generic food sharing in tamarins. International
    Journal of Primatology 20:231-236

Feistner ATC, Price EC (2000) Food sharing in black lion tamarins (*Leontopithecus
    chrysopygus*). American Journal of Primatology 52:47-54

Ferrari SF (1987) Food transfer in a wild marmoset group. Folia Primatologica 48:203-
    206

Ferrari SF (1992) The care of infants in a wild marmoset (*Callithrix flaviceps*) group.
    American Journal of Primatology 26:109-118

Fish JL, Lockwood CA (2003) Dietary constraints on encephalization in primates.

American Journal of Physical Anthropology 120:171-181

Flack JC, de Waal FBM (2000) 'Any animal whatever' - Darwinian building blocks of

morality in monkeys and apes. Journal Of Consciousness Studies 7:1-29

Flombaum JI, Santos LR (2005) Rhesus monkeys attribute perceptions to others.

Current Biology 15:447-452

Foot P (2001) Natural goodness. Oxford University Press, Oxford

Forss SIF (2009) Social learning and independent exploration in immature orangutans

Pongo abelii. MSc thesis. In: Anthropological Institute and Museum, vol

Masters. University of Zurich, Zurich

Forss SIF, van Noordwijk MA, Jaeggi AV, Meulman EM, van Schaik CP (2009) Social

construction of the feeding niche in orang-utans: a comparative study. Folia

Primatologica 80:117-118

Fox GJ (1972) Some comparisons between siamang and gibbon behaviour. Folia

Primatologica 18:122-39

Fragaszy D, Visalberghi E, Fedigan L (2004) The complete capuchin: The biology of

the genus *Cebus*. Cambridge University Press, Cambridge

Fragaszy DM, Feuerstein JM, Mitra D (1997) Transfers of food from adults to infants in

tufted capuchins (*Cebus apella*). Journal of Comparative Psychology 111:194-

200

Fragaszy DM, Mason WA (1983) Comparisons of feeding behavior in captive squirrel

and titi monkeys (*Saimiri sciureus* and *Callicebus moloch*). Journal of

Comparative Psychology 97:310-326

Frank RH (1988) Passions within reason: the strategic role of the emotions. Norton, New York

Fraser ON, Schino G, Aureli F (2008) Components of relationship quality in chimpanzees. Ethology 114:834-843

Fruth B, Hohmann G (2002) How bonobos handle hunts and harvests: Why share food? In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge Univ Press, New York, pp 231-243

Gaechter S, Herrmann B, Thoeni C (in press) Culture and cooperation versus punishment in humans. Philosophical Transactions of the Royal Society B-Biological Sciences

Gallup GG, Jr., Platek SM (2002) Cognitive empathy presupposes self-awareness: Evidence from phylogeny, ontogeny, neuropsychology, and mental illness. Behavioral and Brain Sciences 25:36-37

Gauthier D (1986) Morals by agreement. Clarendon Press, Oxford

Gibson KR (1986) Cognition, brain size and the extraction of embedded food resources. In: Else J, Lee PC (eds) Primate ontogeny, cognition and social behaviour. Cambridge University Press, Cambridge

Gilby IC (2006) Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. Animal Behaviour 71:953-963

Gilby IC, Emery Thompson M, Ruane JD, Wrangham RW (in press) No evidence of short-term exchange of meat for sex among chimpanzees. Journal of Human Evolution

Gilby IC, Wilson MW, Mohlenhoff KA, Pusey AE (2009) The function of coalitionary aggression among wild chimpanzees. American Journal of Physical Anthropology Suppl. 48:133

Gintis H, Henrich J, Bowles S, Boyd R, Fehr E (2008) Strong reciprocity and the roots of human morality. Social Justice Research 21:241-253

Goette L, Huffman D, Meier S (2006) The impact of group membership on cooperation and norm enforcement: Evidence using random assignment to real social groups. The American Economic Review 96:212-216

Goldizen AW (1989) Social relationships in a cooperatively polyandrous group of tamarins (*Saguinus fuscicollis*). Behavioral Ecology and Sociobiology 24:79-89

Gomes CM, Boesch C (2009) Wild chimpanzees exchange meat for sex on a long-term basis. PLOS ONE 4:e5116

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge

Gore MA (1993) Effects of food distribution on foraging competition in Rhesus monkeys, *Macaca mulatta*, and Hamadryas baboons, *Papio hamadryas*. Animal Behaviour 45:773-786

Groves CP (2001) Primate taxonomy. Smithsonian Institution Press, Washington DC

Grueter CC (2009) Determinants of modular societies in snub-nosed monkeys (*Rhinopithecus bieti*) and other Asian colobines. PhD thesis. In, vol PhD. University of Zurich, Zurich

Grueter CC, van Schaik CP (2009) Sexual size dimorphism in Asian colobines revisited. American Journal of Primatology 71:609-616

Gursky S (2000) Allocare in a nocturnal primate: Data on the spectral tarsier, *Tarsius spectrum*. Folia Primatologica 71:39-54

Gurven M (2004) To give and to give not: The behavioral ecology of human food transfers. Behavioral and Brain Sciences 27:543-583

Gurven M, Hill K (2009) Why do men hunt? A reevaluation of "man the hunter" and the sexual division of labor. Current Anthropology 50:51-74

Gurven M, Hill K, Kaplan H, Hurtado A, Lyles R (2000) Food transfers among Hiwi foragers of Venezuela: Tests of reciprocity. Human Ecology 28:171-218

Haidt J (2001) The emotional dog and its rational tail: A social intuitionist approach to moral judgment. Psychological Review 108:814-834

Haidt J (2007) The new synthesis in moral psychology. Science 316:998-1002

Haley KJ, Fessler DMT (2005) Nobody's watching? Subtle cues affect generosity in an anonymous economic game. Evolution and Human Behavior 26:245-256

Hamilton IM (2002) Kleptoparasitism and the distribution of unequal competitors. Behavioral Ecology 13:260-267

Hamilton WD (1964) Genetical evolution of social behaviour I. Journal of Theoretical Biology 7:1-16

Harcourt H, de Waal FBM (1992) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford

Harding RSO (1973) Predation by a troop of Olive baboons (*Papio anubis*). American Journal of Physical Anthropology 38:587-591

Hare B, Kwetuenda S (2010) Bonobos voluntarily share their own food with others. Current Biology 20:R230-R231

Hare B, Melis AP, Woods V, Hastings S, Wrangham R (2007) Tolerance allows
    bonobos to outperform chimpanzees on a cooperative task. Current Biology
    17:619 - 623

Hare B, Tomasello M (2004) Chimpanzees are more skilful in competitive than in
    cooperative cognitive tasks. Animal Behaviour 68:571-581

Hattori Y, Kuroshima H, Fujita K (2005) Cooperative problem solving by tufted
    capuchin monkeys (*Cebus apella*): Spontaneous division of labor,
    communication, and reciprocal altuism. Journal of Comparative Psychology
    119:335-342

Hauser MD (2006) Moral minds: How nature designed ou runiversal sense of right and
    wrong. Ecco, New York

Hauser MD, Chen MK, Chen F, Chuang E (2003) Give unto others: genetically
    unrelated cotton-top tamarin monkeys preferentially give food to those who
    altruistically give food back. Proceedings of the Royal Society B - Biological
    Sciences 279:2363-2370

Hauser MD, Marler P (1993) Food-associated calls in Rhesus macaques (Macaca
    mulatta) .2. Costs and benefits of call production and suppression. Behavioral
    Ecology 4:206-212

Hearn JP, Lunn SF (1975) The reproductive biology of the marmoset monkey,
    Callithrix jacchus. Laboratory Animal Handbook 6:191-204

Hemelrijk CK (1994) Support for being groomed in long-tailed macaques, *Macaca
    fascicularis*. Animal Behaviour 48:479-481

Hemelrijk CK, Meier C, Martin RD (1999) 'Friendship' for fitness in chimpanzees?
    Animal Behaviour 58:1223-1229

Henrich J, Ensminger J, McElreath R, Barr A, Barrett C, Bolyanatz A, Cardenas JC, Gurven M, Gwako E, Henrich N, Lesorogol C, Marlowe F, Tracer D, Ziker J (2010) Markets, religion, community size, and the evolution of fairness and punishment. Science 327:1480-1484

Heschl A, Burkart JM (2006) A new mark test for mirror self-recognition in non-human primates. Primates 47:187-198

Heyes CM (1998) Theory of mind in nonhuman primates. Behavioral and Brain Sciences 21:101-114

Heymann EW (1996) Social behavior of wild moustached tamarins, *Saguinus mystax*, at the Estacion Biologica Quebrada Bianco, Peruvian Amazonia. American Journal of Primatology 38:101-113

Hikami K, Hasegawa Y, Matsuzawa T (1990) Social transmission of food preferences in Japanese monkeys (*Macaca fuscata*) after mere exposure or aversion training. Journal of Comparative Psychology 104:233-237

Hiraiwa-Hasegawa M (1990a) A note on the ontogeny of feeding. In: Nishida T (ed) The chimpanzees of the Mahale Mountains: Sexual and life history strategies. University of Tokyo Press, Tokyo, pp 277-283

Hiraiwa-Hasegawa M (1990b) Role of food sharing between mother and infant in the ontogeny of feeding behavior. In: Nishida T (ed) The chimpanzees of the Mahale Mountains: Sexual and life history strategies. University of Tokyo Press, Tokyo, pp 267-275

Hirata S, Celli ML (2003a) Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. Animal Cognition 6:235-244

Hirata S, Celli ML (2003b) Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. Animal Cognition 6:235-44

Hoage RJ (1982) Social and physical maturation in captive lion tamarins: *Leontopithecus rosalia rosalia* (Primates: Callitrichidae). Smithsonian Contributions to Zoology 354

Hockings KJ, Humle T, Anderson JR, Biro D, Sousa C, Ohashi G, Matsuzawa T (2007) Chimpanzees share forbidden fruit. PLoS ONE 2:e886

Hohmann G, Fruth B (1993) Field observations on meat sharing among bonobos (*Pan paniscus*). Folia Primatologica 60:225-229

Hohmann G, Fruth B (2002) Dynamics in social organization of bonobos (*Pan paniscus*). In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge Univ Press, New York, pp 138-150

Hohmann G, Fruth B (2008) New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. Folia Primatologica 79:103-110

Homburg I (1997) Ökologie und Sozialverhalten einer Gruppe von Weissgesicht-Sakis (*Pithecia pithecia pithecia* Linnaeus 1766) im Estado Bolívar, Venezuela. PhD Thesis. In. Universität Bielefeld, Bielefeld

Horr DA (1977) Orang-utan maturation: Growing up in a female world. In: Chevalier-Skolnikoff S, Poirier FS (eds) Primate bio-social development: biological, social and ecological determinants. Garland Publishing, Inc., New York, pp 289-321

Hosaka K, Nishida T, Hamai M, Matsumoto-Oda A, Uehara S (2001) Predation of mammals by the chimpanzees of the Mahale Mountains, Tanzania. In: All apes

great and small. Volume 1: African apes. Kluwer Acad/Plenum, New York, pp 107-130

Hrdy S (2009) Mothers and others: The evolutionary origins of mutual understanding. Harvard University Press, Cambridge

Huck M, Lottker P, Heymann EW (2004) The many faces of helping: Possible costs and benefits of infant carrying and food transfer in wild moustached tamarins (*Saguinus mystax*). Behaviour 141:915-934

Hume D (2003 [1739-1740]) A treatise of human nature. Dover, Mineola, NY

Humle T, Snowdon C, Matsuzawa T (2009) Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. Animal Cognition 12:37-48

Humle T, Snowdon CT (2008a) Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins, *Saguinus oedipus*. Animal Behaviour 75:267-277

Humle T, Snowdon CT (2008b) Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins, Saguinus oedipus. Animal Behaviour 75:267-277

Hunt KD, McGrew WC (2002) Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge Univ Press, New York, pp 35-51

Hurvich CM, Tsai C-L (1989) Regression and time series model selection in small samples. Biometrika 76:297-307

Huxley TH (1989 [1894]) Evolution and ethics. Princeton University Press, Princeton

Inoue-Nakamura N (2001) Mirror self-recognition in primates: An ontogenetic and a phylogenetic approach. In: Primate origins of human cognition and behavior. Springer, Tokyo, pp 297-312

Izawa K (1978) A field study of the ecology and behavior of the black-mantle tamarin (*Saguinus nigricollis*). Primates 19:241-274

Jaeggi AV, Burkart JM, van Schaik CP (in press) On the psychology of cooperation in humans and other primates: Combining the natural history and experimental evidence of prosociality. Philosophical Transactions of the Royal Society B-Biological Sciences

Jaeggi AV, Dunkel LP, van Noordwijk MA, Wich SA, Sura AAL, van Schaik CP (2010a) Social learning of diet and foraging skills among wild immature Bornean orangutans (*Pongo pygmaeus wurmbii*): Implications for culture. American Journal of Primatology 72:62-71

Jaeggi AV, Stevens JMG, van Schaik CP (2010b) Tolerant food sharing and reciprocity is precluded by despotism in bonobos but not chimpanzees. American Journal of Physical Anthropology:DOI 10.1002/ajpa.21288

Jaeggi AV, van Noordwijk MA, van Schaik CP (2008) Begging for information: Mother-offspring food sharing among wild Bornean orangutans. American Journal of Primatology 70:533-541

Jaeggi AV, van Schaik CP (in review) The evolution of food sharing among primates: Valuable relationships and reciprocal exchange.

Jay P (1965) The common langur of north India. In: DeVore I (ed) Primate behaviour: Field studies of monkeys and apes. Holt, Rinehart & Winston, New York, pp 197-249

Jensen K (in press) Coercion and the "dark side" of cooperation. Philosophical

Transactions of the Royal Society B-Biological Sciences

Jensen K, Hare B, Call J, Tomasello M (2006) What's in it for me? Self-regard

precludes altruism and spite in chimpanzees. Proceedings of the Royal Society

B-Biological Sciences 273:1013-1021

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends in

Ecology & Evolution 19:101-108

Joyce SM, Snowdon CT (2007) Developmental changes in food transfers in cotton-top

tamarins (*Saguinus oedipus*). American Journal of Primatology 69:955-965

Jurke MH, Pryce CR (1994) Parental and infant behavior during early periods of infant

care in Goeldis monkey, *Callimico goeldii*. Animal Behaviour 48:1095-1112

Kano T (1980) Social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba -

a preliminary report. Journal of Human Evolution 9:243-260

Kant I (1994 [1785]) Grundlegung zur Metaphysik der Sitten. Reclam, Stuttgart

Kaplan H, Gurven M (2005) The natural history of human food sharing and

cooperation: A review and a new multi-individual approach to the negotiation of

norms. In: Gintis H, Bowles S, Boyd R, Fehr E (eds) Moral sentiments and

material interests: The foundations of cooperation in economic life. MIT Press,

Cambridge, pp 75-113

Kaplan HS, Hooper PL, Gurven M (2009) The evolutionary and ecological roots of

human social organization. Philosophical Transactions of the Royal Society B-

Biological Sciences 364:3289-3299

Kasper C, Voelkl B, Hub L (2008) Tolerated mouth-to-mouth food transfers in common

marmosets. Primates 49:153-156

Kavanagh M (1972) Food-sharing behavior within a group of douc monkeys (*Pygathrix nemaeus nemaeus*). Nature 239:406-7

Kawanaka K (1982) Further studies on predation by chimpanzees of the Mahale Mountains. Primates 23:364-384

Kitcher P (1985) Vaulting ambition: Sociobiology and the quest for human nature. MIT Press, Cambridge, MA

Kitcher P (1998) Psychological altruism, evolutionary origins, and moral rules. Philosophical Studies 89:283-316

Kitcher P (2003) The Mendelian mirror: philosophical reflections on biolgoy. Oxford University Press, New York

Kitcher P (2005) Biology and ethics. In: Copp D (ed) The Oxford handbook of ethical theory. Oxford University Press, Oxford

Kitcher P (2006a) Ethics and evolution: how to get here from there. In: de Waal FBM (ed) Primates and philosophers: how morality evolved. Princeton University Press, Princeton

Kitcher P (2006b) Prospects for a naturalistic ethics. In: Gesellschaft für analytische Philosophie, Berlin

Klein RG (1999) The human career: human biological and cultural origins. University of Chicago Press, Chicago

Koski SE, Sterck EHM (2009) Empathic chimpanzees: A proposal of the levels of emotional and cognitive processing in chimpanzee empathy. European Journal of Developmental Psychology 7:38 - 66

Koyama NF, Caws C, Aureli F (2006) Interchange of grooming and agonistic support in chimpanzees. International Journal of Primatology 27:1293-1309

Krakauer E, van Schaik CP (2005) Independent and social learning in the development

of aye-aye tap-foraging skills. American Journal of Physical Anthropology

Suppl. 40:132-133

Kühme W (1965) Communal food distribution and division of labour in African hunting

dogs. Nature 205:443-4

Kummer H, Cords M (1991) Cues of ownership in long-tailed macaques, *Macaca

fascicularis*. Animal Behaviour 42:529-549

Kuroda S (1984) Interaction over food among pygmy chimpanzees. In: Susman RL (ed)

The pygmy chimpanzee: Evolutionary biology and behavior. Plenum Press, New

York, pp 301-324

Kuroda S, Suzuki S, Nishihara T (1996) Preliminary report on predatory behavior and

meat sharing in Tschego chimpanzees (*Pan troglodytes troglodytes*) in the

Ndoki Forest, northern Congo. Primates 37:253-259

Lakshminarayanan VR, Santos LR (2008) Capuchin monkeys are sensitive to others'

welfare. Current Biology 18:R999-R1000

Laland KN, Galef B (2009) The question of animal culture. Harvard University Press,

Cambridge MA

Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on

cooperation in wild chimpanzees. Proceedings of the National Academy of

Sciences of the United States of America 104:7786-7790

Langergraber KE, Mitani JC, Vigilant L (2009) Kinship and social bonds in female

chimpanzees (*Pan troglodytes*). American Journal of Primatology 71:840-851

Lehmann L, Rousset F (in press) How ecology / life history promotes or hinders the evolution of cooperation. Philosophical Transactions of the Royal Society B-Biological Sciences

Lewis RAJ (2002) Beyond dominance: The importance of leverage. Quarterly Review of Biology 77:149-164

Lonsdorf EV (2006) What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? Animal Cognition 9:36-46

Lorenz K (1965) Evolution and the modification of behavior. Chicago University Press, Chicago

Lorenz R (1969) Notes on the care, diet and feeding habits of Goeldi's monkey *Callimico goeldii*. International Zoo Yearbook 9:150-155

Lorenz R (1972) Management and reproduction of the goeldi's monkey *Callimico goeldii* (Thomas, 1904) Callimiconidae, Primates. In: Bridgwater DD (ed) Proceedings of the wild animal propagation trust golden lion marmoset conference. Wild Animal Propagation Trust, Wheeling, pp 92-109

MacDonald DW, Sillero-Zubiri C (2004) Biology and conservation of wild canids. In. Oxford University Press, Oxford

Majolo B, Ames K, Brumpton R, Garratt R, Hall K, Wilson N (2006) Human friendship favours cooperation in the iterated prisoner's dilemma. Behaviour 143:1383-1395

Manser MB, Avey G (2000) The effect of pup vocalisations on food allocation in a cooperative mammal, the meerkat (*Suricata suricatta*). Behavioral Ecology and Sociobiology 48:429-437

Manson JH, Wrangham R (1991) Intergroup aggression in chimpanzees and humans. Current Anthropology 32:369-390

Marlowe FW (2004) What explains Hadza food sharing? Research in Economic Anthropology 23:69-88

Marlowe FW (2007) Hunting and gathering: The human sexual division of foraging labor. Cross-cultural research 41:170-195

Marlowe FW (2009) Hadza cooperation. Human Nature - An Interdisciplinary Biosocial Perspective 20:417-430

Marlowe FW, Berbesque JC, Barr A, Barrett C, Bolyanatz A, Cardenas JC, Ensminger J, Gurven M, Gwako E, Henrich J, Henrich N, Lesorogol C, McElreath R, Tracer D (2008) More "altruistic" punishment in larger societies. Proceedings of the Royal Society B 275:587-592

Mason WA, Hollis JH (1962) Communication between young rhesus macaques. Animal Behaviour 10:211-221

Massen JJM, van den Berg LM, Spruijt BM, Sterck EHM (2010) Generous leaders and selfish underdogs: Pro-sociality in despotic macaques. PLoS ONE 5:e9734

Matsubara M, Funakoshi M (2001) Observation of a wild Japanese macaque mother pacifying her distressed infant with an acorn. Primates 42:171-173

Matsumoto-Oda A (2002) Social relationships between cycling females and adult males in Mahale chimpanzees. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge Univ Press, New York, pp 168-180

McGrew WC (1975) Patterns of plant food sharing by wild chimpanzees. In: Kondo S, Kawai M, Ehara A (eds) Contemporary primatology, proceedings of the fifth international congress of primatology. S. Karger, Basel, pp 304-309

Mech LD, Wolf PC, Packard JM (1999) Regurgitative food transfer among wild wolves. Canadian Journal of Zoology-Revue Canadienne De Zoologie 77:1192-1195

Melis AP, Hare B, Tomasello M (2008) Do chimpanzees reciprocate received favours? Animal Behaviour 76:951-962

Melis AP, Semmann D (in press) How is human cooperation different? Philosophical Transactions of the Royal Society B-Biological Sciences

Milinski M, Semmann D, Krambeck HJ (2002) Reputation helps solve the 'tragedy of the commons'. Nature 415:424-426

Mill JS (1987 [1861]) Utilitarianism. Penguin, London

Mitani JC (2006) Reciprocal exchange in chimpanzees and other primates. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolution. Springer, New York, pp 107-119

Mitani JC (2009) Cooperation and competition in chimpanzees: Current understanding and future challenges. Evolutionary Anthropology 18:215-227

Mitani JC, Watts DP (1999) Demographic influences on the hunting behavior of chimpanzees. American Journal of Physical Anthropology 109:439-454

Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? Animal Behaviour 61:915-924

Moller AP, Cuervo JJ (2000) The evolution of paternity and paternal care in birds. Behavioral Ecology 11:472-485

Moore J (1984) The evolution of reciprocal sharing. Ethology and Sociobiology 5:5-14

Morand-Ferron J, Sol D, Lefebvre L (2007) Food stealing in birds: brain or brawn?

       Animal Behaviour 74:1725-1734

Mundry R, Nunn CL (2009) Stepwise model fitting and statistical inference: Turning

       noise into signal pollution. American Naturalist 173:119-123

Nakamura M, Itoh N (2001) Sharing of wild fruits among male chimpanzees: Two cases

       from Mahale, Tanzania. Pan Africa News 8:28-31

Nash LT (1991) Development of food sharing in captive infant *Galago senegalensis*

       braccatus. Primatology Today:181-182

Nash LT (1993) Juveniles in nongregarious primates. In: Pereira ME, Fairbanks LA

       (eds) Juvenile primates: Life history, development and behavior. Oxford

       University Press, New York, pp 119-137

Nettelbeck AR (1998) Observations on food sharing in wild lar gibbons (*Hylobates lar*).

       Folia Primatologica 69:386-391

Newton-Fisher NE (1999) Termite eating and food sharing by male chimpanzees in the

       Budongo Forest, Uganda. African Journal of Ecology 37:369-371

Neyman PF (1980) Ecology and social organization of the cotton-top tamarin (*Saguinus*

       oedipus). PhD Thesis. In. University of California, Berkeley

Nichols S (2004) Sentimental rules: on the natural foundations of moral judgements.

       Oxford University Press, Oxford

Nishida T (1970) Social behavior and relationship among wild chimpanzees of the

       Mahali mountains. Primates 11:47-87

Nishida T (1983) Alloparental behavior in wild chimpanzees of the Mahale Mountains,

       Tanzania. Folia Primatologica 41:1-33

Nishida T, Hasegawa T, Hayaki H, Takahata Y, Uehara S (1992) Meat-sharing as a
    coalition strategy by an alpha male chimpanzee? In: Nishida T, McGrew WC,
    Marler P, Pickford M, De Waal FBM (eds) Topics in primatology. Volume 1:
    Human origins. University of Tokyo Press, Tokyo, pp 159-174

Nishida T, Turner LA (1996) Food transfer between mother and infant chimpanzees of
    the Mahale Mountains National Park, Tanzania. International Journal of
    Primatology 17:947-968

Nishida T, Uehara S, Nyundo R (1979) Predatory behavior among wild chimpanzees of
    the Mahale Mountains. Primates 20:1-20

Nissen HW, Crawford MP (1936) A preliminary study of food-sharing behavior in
    young chimpanzees. Journal of Comparative Psychology 22:383-419

Noë R (2006) Cooperation experiments: coordination through communication versus
    acting apart together. Animal Behaviour 71:1-18

Noë R, de Waal FBM, van Hooff JARAM (1980) Types of dominance in a chimpanzee
    colony. Folia Primatologica 34:90-110

Noë R, Hammerstein P (1994) Biological markets - Supply and demand determine the
    effect of partner choice in cooperation, mutualism and mating. Behavioral
    Ecology and Sociobiology 35:1-11

Noë R, Sluijter A (1995) Which adult male savanna baboons form coalitions?
    International Journal of Primatology 16:77-105

Nowak MA (2006) Five rules for the evolution of cooperation. Science 314:1560-1563

Nowell AA, Fletcher AW (2006) Food transfers in immature wild western lowland
    gorillas (*Gorilla gorilla gorilla*). Primates 47:294-299

Omedes A (1981) Behavioural repertoire of adult silvery marmosets *Callithrix a. argentata* and *Callithrix a. melanura*. Miscellania Zoologica 7:193-211

Pagel M, Meade A BayesTraits. In, 1.0 edn. Reading Evolutionary Biology Group, www.evolution.rdg.ac.uk

Pagel M, Meade A (2006) Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. American Naturalist 167:808-825

Palombit RA (1999) Infanticide and the evolution of pair bonds in nonhuman primates. Evolutionary Anthropology 7:117-129

Pandit SA, van Schaik CP (2003) A model for leveling coalitions among primate males: toward a theory of egalitarianism. Behavioral Ecology and Sociobiology 55:161-168

Panksepp J (2004) Affective neuroscience: The foundations of human and animal emotions. Oxford University Press, Oxford

Paradis E (2006) Analysis of phylogenetics and evolution with R. Springer, New York

Paradis E, Bolker BM, Claude J, Cuong HS, Desper R, Durand B, Dutheil J, Gascuel O, Jobb G, Heibl C, Lawson D, Lefort V, Legendre P, Lemon J, Noel Y, Nylander J, Opgen-Rhein R, Strimmer K, de Vienne D (2009) Analyses of phylogenetics and evolution. In:

Pastor-Nieto R (2001) Grooming, kinship, and co-feeding in captive spider monkeys (*Ateles geoffroyi*). Zoo Biology 20:293-303

Peacock MS, Schefczyk S, Schaber P (2005) Altruism and the indispensability of motives. Analyse & Kritik 27:188-196

Pele M, Dufour V, Thierry B, Call J (2009) Token transfers among great apes (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes*): Species differences, gestural requests and reciprocal exchange Journal of Comparative Psychology 123:375-384

Penn DC, Povinelli DJ (2007) On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind'. Philosophical Transactions of the Royal Society B-Biological Sciences 362:731-744

Perebom ZJJM, Stevens JMG (2008) International studbook for the bonobo *Pan paniscus* SCHWARZ 1929. Royal Zoological Society of Antwerp, Antwerp, Belgium

Perry S, Rose L (1994) Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. Primates 35:409-415

Peterhans S (2006) Food sharing in three groups of chimpanzees (*Pan troglodytes*) at Gänserndorf. MSc thesis. In, vol Master. University of Zurich, Zurich

Phillips W, Barnes JL, Mahajan N, Yamaguchi M, Santos LR (2009) 'Unwilling' versus 'unable': capuchin monkeys' (*Cebus apella*) understanding of human intentional action. Developmental Science 12:938-945

Pika S, Mitani J (2006) Referential gestural communication in wild chimpanzees (*Pan troglodytes*). Current Biology 16:R191-R192

Pinheiro JC, Bates D, DebRoy S, Sarkar D, R core team (2008) nlme: linear and non-linear mixed effects models. In, 3.1-90 edn

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York

Plavcan JM, van Schaik CP, Kappeler PM (1995) Competition, coalitions and canine size in primates. Journal of Human Evolution 28:245-276

Plotnik JM, de Waal FBM, Reiss D (2006) Self-recognition in an Asian elephant. Proceedings of the National Academy of Sciences of the United States of America 103:17053-17057

Price EC, Feistner ATC (1993) Food sharing in lion tamarins - tests of 3 hypotheses. American Journal of Primatology 31:211-221

Price EC, Feistner ATC (2001) Food sharing in pied bare-faced tamarins (*Saguinus bicolor bicolor*): Development and individual differences. International Journal of Primatology 22:231-241

Prior H, Schwarz A, Güntürkün O (2008) Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. PLoS Biology 6:e202

Pruetz JD, Bertolani P (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Current Biology 17:412-417

R Development Core Team (2009) R: A language and environment for statistical computing. In. R Foundation for Statistical Computing, Vienna, Austria

R Development Core Team (2010) R: A language and environment for statistical computing. In. R Foundation for Statistical Computing, Vienna, Austria

Rao N, Stewart SM (1999) Cultural influences on sharer and recipient behavior - Sharing in Chinese and Indian preschool children. Journal of Cross-Cultural Psychology 30:219-241

Rapaport LG (1999) Provisioning of young in golden lion tamarins (Callitrichidae, *Leontopithecus rosalia*): A test of the information hypothesis. Ethology 105:619-636

Rapaport LG (2001) Food transfer among adult lion tamarins: Mutualism, reciprocity or one-sided relationships? International Journal of Primatology 22:611-629

Rapaport LG (2006a) Parenting behaviour: Babbling bird teachers? Current Biology 16:R675-R677

Rapaport LG (2006b) Provisioning in wild golden lion tamarins (*Leontopithecus rosalia*): benefits to omnivorous young. Behavioral Ecology 17:212-221

Rapaport LG, Brown GR (2008) Social influences on foraging behaviour in young nonhuman primates: Learning what, where and how to eat. Evolutionary Anthropology 17:189-201

Rapaport LG, Ruiz-Miranda CR (2002) Tutoring in wild golden lion tamarins. International Journal of Primatology 23:1063-1070

Rapaport LG, Ruiz-Miranda CR (2006) Ontogeny of provisioning in two populations of wild golden lion tamarins (*Leontopithecus rosalia*). Behavioral Ecology and Sociobiology 60:724-735

Reiss D, Marino L (2001) Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. Proceedings of the National Academy of Sciences of the United States of America 98:5937-5942

Reynolds V (2005) The chimpanzees of the Budongo forest: Ecology, behaviour and conservation. Oxford Univ Press, New York

Ridley M (1996) The origins of virtue: human instincts and the evolution of cooperation. Viking, London

Rigdon M, Ishii K, Watabe M, Kitayama S (2009) Minimal social cues in the dictator game. Journal of Economic Psychology 30:358-367

Roberts G (2008) Evolution of direct and indirect reciprocity. Proceedings of the Royal
      Society B-Biological Sciences 275:173-179

Rose LM (1997) Vertebrate predation and food sharing in *Cebus* and *Pan*. International
      Journal of Primatology 18:727-765

Rose LM (2001) Meat and the early human diet: Insights from Neotropical primate
      studies. In: Stanford CB, Bunn HT (eds) Meat-eating and human evolution.
      Oxford Univ Press, New York, pp 141-159

Roush RS, Snowdon CT (2000) Quality, quantity, distribution and audience effects on
      food calling in cotton-top tamarins. Ethology 106:673-690

Roush RS, Snowdon CT (2001) Food transfer and development of feeding behavior and
      food-associated vocalizations in cotton-top tamarins. Ethology 107:415-429

Rowe N (1996) The pictorial guide to the living primates. Pogonias Press, Charlestown

Ruiz-Miranda CR, Kleiman DG, Dietz JM, Moraes E, Grativol AD, Baker AJ, Beck BB
      (1999) Food transfers in wild and reintroduced golden lion tamarins,
      Leontopithecus rosalia. American Journal of Primatology 48:305-320

Ruse M (1986) Taking Darwin seriously: an naturalistic approach to philosophy.
      Blackwell, Oxford

Ruse M (2009) The biological sciences can act as a ground for ethics. In: Ayala FJ, Arp
      R (eds) Contemporary debates in philosophy of biology. Wiley, Chichester UK

Russell YI, Call J, Dunbar RIM (2008) Image scoring in great apes. Behavioural
      Processes 78:108-111

Ryan MJ (2009) The evolution of behavior, and integrating it towards a complete and
      correct understanding of behavioral biology. In: Bolhuis JJ, Verhulst S (eds)

Tinbergen's legacy: Function and mechanism in behavioral biology. Cambridge University Press, Cambridge

Saito A, Izumi A, Nakamura K (2008) Food transfer in common marmosets: parents change their tolerance depending on the age of offspring. American Journal of Primatology 70:999-1002

Sannen A, Van Elsacker L, Eens M (2004) Effect of spatial crowding on aggressive behavior in a bonobo colony. Zoo Biology 23:383-395

Savage A, Snowdon CT, Giraldo LH, Soto LH (1996) Parental care patterns and vigilance in wild cotton-top tamarins (*Saguinus oedipus*). In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive radiations of neotropical primates. Plenum Press, New York, pp 187-199 & 539

Schaub H (1996) Testing kin altruism in long-tailed macaques (*Macaca fascicularis*) in a food-sharing experiment. International Journal of Primatology 17:445-467

Schessler T, Nash LT (1977) Food sharing among captive gibbons (*Hylobates lar*). Primates 18:677-689

Schino G (2007) Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. Behavioral Ecology 18:115-120

Schino G, Aureli F (2008) Trade-offs in primate grooming reciprocation: testing behavioural flexibility and correlated evolution. Biological Journal of the Linnean Society 95:439-446

Schino G, Aureli F (2009) Reciprocal altruism in primates: Partner choice, cognition, and emotions. Advances in the Study of Behavior 39:45-69

Schradin C, Anzenberger G (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: an experimental analysis. Animal Behaviour 62:289-295

Seyfarth RM, Cheney DL (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. Nature 308:541-543

Silk JB (1978) Patterns of food sharing among mother and infant chimpanzees at Gombe national park, Tanzania. Folia Primatologica 29:129-141

Silk JB (1979) Feeding, foraging, and food sharing behavior of immature chimpanzees. Folia Primatologica 31:123-142

Silk JB (2002) Using the 'F'-word in primatology. Behaviour 139:421-446

Silk JB (2006) Practicing Hamilton's rule: Kin selection in primate groups. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans. Springer, Berlin

Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaro J, Schapiro SJ (2005) Chimpanzees are indifferent to the welfare of unrelated group members. Nature 437:1357-1359

Silk JRRLL (2007) Empathy, sympathy, and prosocial preferences in primates. In: Dunbar RIM, Barrett L (eds) Oxford handbook of evolutionary psychology. Oxford Univ Press, New York, pp 115-126

Slocombe KE, Newton-Fisher NE (2005) Fruit sharing between wild adult chimpanzees (*Pan troglodytes schweinfurthii*): A socially significant event? American Journal of Primatology 65:385-391

Smith A (2002 [1759]) The theory of moral sentiments. Cambridge University Press, Cambridge

Smith EA, Bliege Bird RL (2005) Costly signaling and cooperative behavior. In: Gintis H, Bowles S, Boyd R, Fehr E (eds) Moral sentiments and material interests: The foundations of cooperation in economic life. MIT Press, Cambridge, MA, pp 115-148

Snowdon CT, Cronin KA (2007) Cooperative breeders do cooperate. Behavioural

Processes 76:138-141

Soares M, Fusani L, Goymann W, Groothuis T, Hau M, Oliveira R (in press)

Endocrinology and levels of cooperation. Philosophical Transactions of the

Royal Society B-Biological Sciences

Sober E, Wilson DS (1998) Unto others: The evolution and psychology of unselfish

behavior. In. Harvard University Press, Cambridge, MA

Stanford CB (1998) The social behavior of chimpanzees and bonobos. Current

Anthropology 39:399-420

Stanford CB (1999) The hunting apes: meat eating and the origins of human behavior.

Princeton Univ Press, Princeton

Starin ED (1978) Food transfer by wild titi monkeys (*Callicebus torquatus torquatus*).

Folia Primatologica 30:145-151

Starin ED (2006) Patterns of food transfer in Temminck's red colobus. Aggressive

Behavior 32:181-186

Stevens JMG, Thierens M, Vervaecke H (2007a) What are you looking at? The social

context of peering behaviour in captive bonobos. In: Dow S, Clark F (eds)

Proceedings of the annual symposium on zoo research: 2006, Colchester Zoo.

The federation of zoological gardens of Great Britain and Ireland, London, pp

170-175

Stevens JMG, Vervaecke H, de Vries H, van Elsacker L (2005) The influence of the

steepness of dominance hierarchies on reciprocity and interchange in captive

groups of bonobos (*Pan paniscus*). Behaviour 142:941-960

Stevens JMG, Vervaecke H, van Elsacker L (2007b) Sex differences in the steepness of

dominance hierarchies in captive bonobo groups. International Journal of

Primatology 28:1417-1430

Stevens JMG, Vervaecke H, van Elsacker L (2008) The bonobo's adaptive potential:

Social relations under captive conditions. In: Furuichi T, Thompson J (eds) The

Bonobos. Behavior, Ecology and Conservation. Springer, New York, pp 19-38

Stevens JR (2004) The selfish nature of generosity: harassment and food sharing in

primates. Proceedings of the Royal Society of London Series B-Biological

Sciences 271:451-456

Stevens JR (2010) Donor payoffs and other-regarding preferences in cotton-top

tamarins (*Saguinus oedipus*). Animal Cognition:DOI 10.1007/s10071-010-0309-

x

Stevens JR, Gilby IC (2004) A conceptual, framework for nonkin food sharing: timing

and currency of benefits. Animal Behaviour 67:603-614

Stevens JR, Hauser MD (2004) Why be nice? Psychological constraints on the

evolution of cooperation. Trends in Cognitive Sciences 8:60-65

Stevens JR, Stephens DW (2002) Food sharing: a model of manipulation by

harassment. Behavioral Ecology 13:393-400

Strum SC (1975) Primate predation: Interim report on the development of a tradition in

a troop of olive baboons. Science 187:755-757

Strum SC (1981) Processes and products of change: Baboon predatory behavior at

Gilgil, Kenya. In: Harding RSO, Teleki G (eds) Omnivorous primates:

Gathering and hunting in human evolution. Columbia University Press, New

York, pp 255-302

Stumpf R (2007) Chimpanzees and bonobos: diversity within and between species. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) Primates in perspective. Oxford Univ Press, New York, pp 321-344

Subiaul F, Vonk J, Okamoto-Barth S, Barth J (2008) Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. Animal Cognition 11:611-623

Surbeck M, Hohmann G (2008) Primate hunting by bonobos at LuiKotale, Salonga National Park. Current Biology 18:R906-R907

Suzuki A (1971) Carnivority and cannibalism observed among forest-living chimpanzees. Journal of the Anthropological Society of Nippon 79:30-48

Tabachnik BG, Fidell LS (2007) Using mulitvariate statistics. Pearson Education Inc., Boston, MA

Tacconi G, Palagi E (2009) Play behavioural tactics under space reduction: social challenges in bonobos, *Pan paniscus*. Animal Behaviour 78:469-476

Takahata Y, Hasegawa T, Nishida T (1984) Chimpanzee predation in the Mahale mountains from August 1979 to May 1982. International Journal of Primatology 5:213-233

Takimoto A, Kuroshima H, Fujita K (2010) Capuchin monkeys (*Cebus apella*) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics. Animal Cognition 13:249-261

Tardif SD, Santos CV, Baker AJ, Van Elsacker L, Feistner ATC, Kleiman DG, Ruiz-Miranda CR, Moura ACA, Passos FC, Price EC, Rapaport LG, De Vleeschouwer K (2002) Infant care in lion tamarins. In: Kleiman DG, Rylands

AB (eds) Lion tamarins: Biology and conservation. Smithsonian Institution
Press, Washington, DC, pp 213-232

Teleki G (1973) The predatory behavior of wild chimpanzees. Bucknell University
Press, Lewisburg, Pennsylvania

Thierry B, Wunderlich D, Gueth C (1989) Possession and transfer of objects in a group
of brown capuchins (*Cebus apella*). Behaviour 110:294-305

Thornton A, McAuliffe K (2006) Teaching in wild meerkats. Science 313:227-229

Thornton A, Raihani NJ (2008) The evolution of teaching. Animal Behaviour 75:1823-
1836

Tinbergen N (1951) The study of instincts. Oxford University Press, Oxford

Tinbergen N (1952) "Derived" activities; their causation, biological significance, origin,
and emancipation during evolution. The Quarterly Review of Biology 27:1-32

Tomasello M, Carpenter M (2007) Shared intentionality. Developmental Science
10:121-125

Tooby J, Cosmides L (2005) Conceptual foundations of evolutionary psychology. In:
Buss DM (ed) The handbook of evolutionary psychology. Wiley, Hoboken NJ

Trivers RL (1971) Evolution of reciprocal altruism. Quarterly Review of Biology 46:35-
57

Trivers RL (2006) Reciprocal altruism: 30 years later. In: Kappeler PM, van Schaik CP
(eds) Cooperation in primates and humans: mechanisms and evolution. Springer,
New York, pp 67-83

Trivers RL (2010) Deceit and self-deception. In: Kappeler PM, Silk JB (eds) Mind the
gap: Tracing the origins of human universals. Springer, Berlin

Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Behavioral Ecology and Sociobiology 6:29-38

Ueno A, Matsuzawa T (2004) Food transfer between chimpanzee mothers and their infants. Primates 45:231-239

Utami SS, van Hooff JARAM (1997) Meat-eating by adult female Sumatran orangutans (*Pongo pygmaeus abelii*). American Journal of Primatology 43:159-165

Vahed K (1998) The function of nuptial feeding in insects: review of empirical studies. Biological Reviews 73:43-78

van Hooff JARAM (1973) A structural analysis of the social behaviour of a semi-captive group of chimpanzees. European Monographs in Social Psychology 4:75-162

van Hooff JARAM, Wensing JAB (1987) Dominance and its behavioral measures in a captive wolf pack. In: Frank HW (ed) Man and wolf. Junk Publishers, Dordrecht, pp 219-252

van Lawick-Goodall J (1968) The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Animal Behaviour Monographs:165-311

van Noordwijk MA, van Schaik CP (2009) Intersexual food transfer among orangutans: do females test males for coercive tendency? Behavioral Ecology and Sociobiology 63:883-890

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative socioecology. The behavioural ecology of humans and other mammals. Blackwell Scientific Publications, Oxford, pp 195-218

van Schaik CP (1999) The socioecology of fission-fusion sociality in orangutans.

Primates 40:69-86

van Schaik CP, Burkart JM (2010) Mind the gap: Cooperative breeding and the

evolution of our unique features. In: Kappeler PM, Silk J (eds) Mind the gap:

Tracing the origins of human universals. Springer, Heidelberg, pp 477-497

van Schaik CP, Fox EA, Sitompul AF (1996) Manufacture and use of tools in wild

Sumatran orangutans - Implications for human evolution. Naturwissenschaften

83:186-188

Vervaecke H, de Vries H, van Elsacker L (2000) Dominance and its behavioral

measures in a captive group of bonobos (*Pan paniscus*). International Journal of

Primatology 21:47-68

Vitale A, Queyras A (1997) The response to novel foods in common marmoset

(*Callithrix jacchus*): The effects of different social contexts. Ethology 103:395-

403

Vonk J, Brosnan SF, Silk JB, Henrich J, Richardson AS, Lambeth SP, Schapiro SJ,

Povinelli DJ (2008) Chimpanzees do not take advantage of very low cost

opportunities to deliver food to unrelated group members. Animal Behaviour

75:1757-1770

Warneken F, Hare B, Melis AP, Hanus D, Tomasello M (2007) Spontaneous altruism

by chimpanzees and young children. PLoS Biology 5:1414-1420

Warneken F, Tomasello M (2006) Altruistic helping in human infants and young

chimpanzees. Science 311:1301-1303

Warneken F, Tomasello M (2009) Varieties of altruism in children and chimpanzees.

Trends in Cognitive Sciences 13:397-402

Watt S (1994) Alloparental behavior in a captive group of spider monkeys (*Ateles geoffroyi*) at the Auckland zoo. International Journal of Primatology 15:135-151

Watts DP (1985) Observations on the ontogeny of feeding behavior in mountain gorillas (*Gorilla gorilla beringei*). American Journal of Primatology 8:1-10

Watts DP (2002) Reciprocity and interchange in the social relationships of wild male chimpanzees. Behaviour 139:343-370

Watts DP, Mitani JC (2002) Hunting and meat sharing by chimpanzees at Ngogo, Kibale National Park, Uganda. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge Univ Press, New York, pp 244-255

Westergaard GC, Haynie MK, Lundquist AL, Suomi SJ (1999) Carrying, sharing, and hand preference in tufted capuchins (*Cebus apella*). International Journal of Primatology 20:153-162

Westergaard GC, Kuhn HE, Babitz MA, Suomi SJ (1998) Aimed throwing as a means of food transfer between tufted capuchins (*Cebus apella*). International Journal of Primatology 19:123-131

Westergaard GC, Suomi SJ (1997) Transfer of tools and food between groups of tufted capuchins (*Cebus apella*). American Journal of Primatology 43:33-41

Westlund K, Ljungberg T, Borefelt U, Abrahamsson C (2000) Post-conflict affiliation in common marmosets (*Callithrix jacchus jacchus*). American Journal of Primatology 52:31-46

White F (1994) Food sharing in wild pygmy chimpanzees (*Pan paniscus*). In: Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N (eds) Current Primatology

Volume II: Social development, learning and behavior, vol 2. Université Louis Pasteur, Strasbourg, pp 1–10

Whitehead JM (1986) Development of feeding selectivity in mantled howling monkeys, *Alouatta palliata*. In: Else DG, Lee PC (eds) Primate ontogeny, cognition and social behaviour. Cambridge University Press, New York, pp 105-117

Wilson C (1976) Food sharing behavior in primates: another species added. Arkansas Academic Scientific Proceedings 30:95-96

Wilson EO (1975) Sociobiology. Harvard University Press, Cambridge MA

Winn RM (1994) Development of behaviour in a young aye-aye (*Daubentonia madagascariensis*) in captivity. Folia Primatologica 62:93-107

Wobber V, Wrangham R, Hare B (2010) Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. Current Biology 20:226-230

Wolovich CK, Evans S, French JA (2008a) Dads do not pay for sex but do buy the milk: food sharing and reproduction in owl monkeys (*Aotus* spp.). Animal Behaviour 75:1155-1163

Wolovich CK, Feged A, Evans S, Green SM (2006) Social patterns of food sharing in monogamous owl monkeys. American Journal of Primatology 68:663-674

Wolovich CK, Perea-Rodriguez JP, Fernandez-Duque E (2008b) Food transfers to young and mates in wild owl monkeys (*Aotus azarai*). American Journal of Primatology 70:211-221

Wolters HJ (1978) Some aspects of role taking behaviour in captive family groups of the cotton-top tamarin *Saguinus oedipus oedipus*. In: Rothe H, Wolters HJ,

Hearn JP (eds) Biology and behaviour of marmosets. Mercke-Druck, Goettingen, West Germany, pp 259-278

Woodburn J (1982) Egalitarian societies. Man 17:431-451

Wrangham RW (1975) The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. In, vol PhD. University of Cambridge, Cambridge

Wright PC (1984) Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In: Small MF (ed) Female primates: studies by women primatologists. Alan R. Liss, Inc., New York, pp 59-75

Wright R (2006) The uses of anthropomorphism. In: de Waal FBM (ed) Primates and philosophers: how morality evolved. Princeton Univ Press, Princeton, pp 83-97

Yamamoto ME, Box HO (1997) The role of non-reproductive helpers in infant care in captive *Callithrix jacchus*. Ethology 103:760-771

Yamamoto S, Humle T, Tanaka M (2009) Chimpanzees help each other upon request. PLoS ONE 4:e7416

Yamamoto S, Tanaka M (2009a) Do chimpanzees (*Pan troglodytes*) spontaneously take turns in a reciprocal cooperation task? Journal of Comparative Psychology 123:242-249

Yamamoto S, Tanaka M (2009b) How did altruism and reciprocity evolve in humans? Perspectives from experiments on chimpanzees (*Pan troglodytes*). Interaction Studies 10:150-182

Yamamoto S, Tanaka M (2010) The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. Animal Behaviour 79:595-602

Yeager C, Kirkpatrick R (1998) Asian colobine social structure: Ecological and evolutionary constraints. Primates 39:147-155

Yoneda M (1984) Ecological study of the saddle-back tamarin (*Saguinus fuscicollis*) in northern Bolivia. Primates 25:1-12

Zahavi A (1987) The theory of signal selection and some of its implications. In: Deflino VP (ed) International symposium of biological evolution. Adriatica Editrice, Bari, pp 305-325

Zhang Z, Su YJ, Chan RCK, Reimann G (2008) A preliminary study of food transfer in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). American Journal of Primatology 70:148-152

Ziltener A (2007) Exploration and innovation in captive chimpanzees (*Pan troglodytes*). MSc thesis. In, vol Master. University of Zurich, Zurich

Zimmermann E (1989) Reproduction, physical growth and behavioral development in slow loris (*Nycticebus coucang*, Lorisidae). Human Evolution 4:171-179

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Vornamen: <u>Adrian</u> Viktor

Geburstdatum: 3. Dezember 1980

Heimatorte: Solothurn und Fulenbach (SO)

Ausbildung

1993-2000   Kantonsschule Hohe Promenade Zürich, Matur Typus B (Latein und Englisch)

2000-2006   Universität Zürich, Studium der Biologie, Hauptfach Anthropologie. Diplomarbeit: „*The role of social learning in the acquisition of foraging skills among wild Bornean orangutans (*Pongo pygmaeus*)* "

2007-2010   Universität Zürich, Promotionsstudium, Hauptfach Anthropologie.

Auszeichnungen

Auszeichnung der Diplomarbeit durch die Mathematisch-naturwissenschaftliche Fakultät der Universität Zürich (2006)

Nachwuchsförderpreis der A.H. Schultz Stiftung (2006)

Preis für den besten Vortrag an der 10. Konferenz der Gesellschaft für Primatologie (2006)

Anstellung und Stipendien während des Promotionsstudiums

Anstellung: UFSP Ethik, Graduiertenprogramm für interdisziplinäre Ethikforschung

Stipendien: Cogito foundation (Projekt S-106/06), A.H. Schultz Stiftung

Weitere Tätigkeiten während des Promotionsstudiums

Lehre: Einzelne Lektionen am Anthropologischen Institut (Bio 209, Bio 213)

Vorträge: Acht Vorträge an internationalen Kongressen

                  Vier Vorträge an externen Seminaren

Publikationen: Zwei Publikationen zur Diplomarbeit (Jaeggi et al. 2008, 2010a)

                  Zwei Publikationen zur Dissertation (Jaeggi et al. 2010b, in press), drei

                  weitere in Vorbereitung

Weiteres: Studentenvertreter am Anthropologischen Institut (2005-2007)

                  Mitglied des Koordinationskommittees der Evaluation des

                  Anthropologischen Instituts (2006-2008)

                  Mitglied des Organisationskommittees des 3. Kongresses der European

                  Federation for Primatology in Zürich (2009)

                  Ko-organisator des Journal Clubs am Anthropologischen Institut (2009-

                  heute)