Abstracts

of

Talks and Posters

Cooperation: Patterns of allogrooming in a capuchin monkey group

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Capuchin monkeys (*Cebus apella*) live in multi-male multi-female social groups consisting of both kin and non-kin conspecifics. Females form linear dominance hierarchies, which are regularly reinforced. Reinforcement may take the form of agonistic confrontations or it can be in the form of non-aggressive bonding through association and servicing such as allogrooming. This study focuses on allogrooming between 5 adult females (age range 7-24 years) in a semi-captive colony of 23 capuchins. Allogrooming was tested against two major hypotheses, firstly, that distribution of grooming shows partnerships in which grooming is preferentially directed, secondly, that there is a relationship between allogrooming and autogrooming over body surface area. Animals have limited time and energy; they could groom all group members little, or concentrate efforts towards a sub-group consisting of specific individuals. To establish social cliques per individual, data are presented for the distribution of allogrooming between adult females. Analysis of the distribution tests two predictions, a.) Grooming is preferentially directed up the dominance hierarchy, b.) Females form preferred grooming partnerships in which grooming is bidirectional. These partnerships will be largely affected by kinship and relative dominance position. Allogrooming may have an important hygienic value, the removal of parasites and substances from the skin and hair. The value of allogrooming may relate to those regions that are difficult to groom oneself, being hard to reach or impossible to see during autogrooming. The prediction tested was that the relationship between body-sites serviced during receipt of allogrooming and autogrooming is inversely correlated. Analysis of observations compared allogrooming with autogrooming in terms of predefined body-sites as evidence for a hygienic function of allogrooming.

Causes and mechanisms for reconciliation: The role of cooperation

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Conflict between group members is a natural manifestation of competition for resources and coordination of activities. The escalation of conflict, however, can have detrimental consequences for the individuals involved and jeopardize cooperation. Conflict management is therefore a critical component of social life. There is strong evidence for post-conflict friendly reunions between former opponents in the vast majority of non-human primates studied in captivity and in the wild. Such reunions have been demonstrated to function as reconciliation by repairing social relationships disturbed by the previous aggressive conflict. The degree of cooperation in the relationship between former opponents is a good predictor of reconciliation frequency in comparisons across dyads of the same group, across groups of the same

species, and across closely related species. Cooperation between two individuals is not, however, assurance for reconciliation because biological markets modulate the relative value of group members. Not only is cooperation an underlying causal force for reconciliation, but it is also at the core of how reconciliation is achieved. The exchange of friendly behavior soon after two individuals have fought requires a high degree of cooperation. The two former opponents are likely to differ in their interest in repairing the relationship, but for reconciliation to occur they need to cooperate. Each partner needs to establish whether a conflict signifies a growing mismatch in the relative value of the relationship or whether it is just a 'hiccup'. Thus, the reconciliation process is a means of communication between former opponents about the state of their relationship by showing their relative interest in repairing it. The study of opponents' emotional responses to post-conflict relationship disturbance can open a new window on the role of cooperation in conflict resolution by providing researchers with the means to infer the opponents' relative interest in reconciliation.

A market for brain size: Biological markets and primate sociality

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The "Machiavellian Intelligence" or "Social Brain" hypothesis states that the need to assess complex polyadic situations within the context of stable social groups formed the major selection pressure on brain size within the primate order. The need to form coalitions against others and build up co-operative alliances is thought to have produced a ratchet-like effect on brain size as ever greater levels of social intelligence were required to cope with the strategies and counter-strategies developed by group mates to further their own ends at the expense of others. However, while adult female chacma baboons form differentiated grooming relationships, cooperative coalitions are exceptionally rare, suggesting that the latter are not, in fact, critical to the development of higher cognitive abilities. Here, we suggest that partner choice is not based on long-term co-operative alliance formation, but instead reflects the operation of an ever-changing market trading system based on grooming and tolerance, and that short-term tactical choices with regard to individual interactions are the key to understanding female sociality. We will further argue that increased social intelligence was initially selected, not in order to cope with complex polyadic coalition scenarios, but to weigh-up an ever changing set of options regarding partner choice on an everyday basis. The need to make tactical decisions regarding the number of partners selected and the benefits to be gained from each may also provide us with some clues as to why apes and monkeys differ cognitively; a difference which is, at present, not well characterized

Do male sooty mangabeys (*Cercocebus atys*) use coalitions as a reproductive tactic?

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Male dominance hierarchies function as queues for mating opportunities in many primates with multi-male groups. Lower ranking males may, however, jump the queue by forming coalitions. This study, conducted over a period of 8 months in the Tai National Park in Ivory Coast, aimed to investigate whether male sooty mangabeys also use coalition formation to improve their access to mates. Data were collected on the adult males of a group with a total membership of 120: 9 'residents' and 14 'non-residents', i.e. males that entered the group during the study period. Resident males exhibited a stable linear hierarchy, but their mating frequencies deviated from the predictions based on the priority-of-access model (ALTMANN 1962, Ann. N.Y. Acad. Sci. 102:338). This was not caused by the formation of coalitions directly aimed at obtaining access to females, as is the case, for example, in baboons. Coalition formation was strongly linked to the mating season, however. The number of immigrations by adult males was positively correlated with the number of females in oestrus. As soon as the influx of non-residents began, the number of coalitions observed increased significantly. Of the 166 coalitions I observed in that period 150 were by residents against non-residents. Coalitions (N = 11) observed during the mating season before immigrations started were mainly against a low-ranking male that subsequently disappeared from the group. While a large proportion of the coalitions was formed by middle-ranking residents, we can conclude that these males aimed at shortening the queue by keeping out strangers and chasing young males out of their group. The deviations of the 'priority-of-access'-model were mainly caused by sneak copulations. Of the 206 copulations by resident males observed, 44 (21%) were by low-ranking residents in the periphery of the group. We observed 54 copulations by non-residents, half of which (27) also took place in the periphery.

Cooperation in chimpanzees: Kinship or mutualism?

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The evolution of cooperation in social animals has been the subject of many discussions as three different mechanisms could be responsible for its appearance. Kin selection would favor the evolution of cooperation between related individuals, while mutualism would explain it between unrelated individuals. The difficulties of showing this in social carnivores has led some authors to suggest that cooperation could be a by-product of group living, and evolve without providing direct benefit to participants. On the other hand, kin-bonded groups have been proposed to evolve as a mean to increase the benefit from cooperation that would develop more easily be-

tween related individuals. Following this logic, chimpanzees (*Pan troglodytes*), a species where many different instances of cooperation have been documented among males, has regularly been proposed to live in male-bonded kin groups. Tests of those ideas on affiliative behaviors in Ngogo chimpanzees have shown that relatedness does not predict them, but that age and rank are important predictors instead. Studies of Taï chimpanzees, which hunt mainly in highly cooperative groups, revealed that relatedness among males is not higher than relatedness among females and that individuals hunting more together do not seem to be more closely related than other dyads. Alternatively it could be shown that meat access increases for hunters more than for non-hunters, and that hunters performing the more crucial hunting roles gained more meat than others. Therefore, present data clearly show s that cooperation in Taï chimpanzee evolved out of mutualism and not kin selection. The importance of mutualism in cooperation in other species will be discussed.

Dispersed male networks' in western gorillas

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Although kin selection theory has been used to explain the biasing of beneficial behaviors or reduced aggression towards relatives living within the same social group, relatively little attention has focused on the possibility of kin-biased interactions occurring between individuals in different social groups. Recent behavioral data from western gorillas indicate that silverback males of this species are unusual in often reacting peacefully during encounters with the males of neighboring groups. This lack of overt aggression between males of different groups is unexpected since inter-group interactions in many primates, including mountain gorillas are usually highly aggressive contests over access to females and may involve physical violence and fatal injuries. In order to see whether kinship might explain the unusual social relations in western gorillas, we investigated the pattern of genetic relationships among 71 individuals in 13 different groups ranging near Mondika Research Center in the Central African Republic and Republic of Congo. Microsatellite genotyping of DNA from hair and feces samples collected at fresh nest sites was used to determine paternity of offspring and to estimate relatedness among individuals. Results indicate that the resident silverback can monopolize paternity over several years, thus producing group offspring that are half-siblings. Males appear to disperse less far than females, and silverback males leading nearby groups are often related. This pattern of reproduction and dispersal suggests the existence of a previously unrecognized 'dispersed male network' social structure in western gorillas.

A negative reaction to unequal reward division in non-human primates

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During the evolution of cooperation, it may have become worthwhile for individuals to compare their own payoffs to those of others, in an effort to increase relative fitness. Humans do so, frequently rejecting payoffs that are perceived as unfair (even if they are advantageous). While there is some variation, this response is widespread across human populations. If a sense of fairness did evolve to promote cooperation, some nonhuman animals may exhibit inequity aversion as well. This is particularly likely in social species with tolerant societies, such that individuals may reasonably expect some equity between themselves and other group members. Here we examine the response of 5 capuchin monkeys and 20 chimpanzees to an unequal distribution of rewards during experimental exchange with a human experimenter. Individuals in pairs alternated exchanges with the experimenter under four conditions: 1) both received the same reward, 2) one received a superior reward, 3) one received a superior reward without exchange (i.e. no work), and 4) a superior reward was present, but not given to a conspecific. Capuchins were significantly less likely to complete an exchange when their partner received a higher-value food item than they, and this response was amplified if the partner received the reward without working for it. Refusals to exchange included refusing to return the token, either ignoring it or throwing it out of the testing area, and refusing to accept the food reward following a completed exchange. Chimpanzees showed a much more variable response, with some individuals showing little or no reaction and some reacting in a similar manner to the capuchins. While the basis of this inequity averse response is unknown (e.g. potentially social emotions, as proposed for humans), negative responses to this type of situation supports a relatively early evolutionary origin of inequity aversion.

Kinship, cooperation, and nepotistic regimes in primates

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The idea that kinship plays a central role in the organization of primate behavior has become almost a truism. In general, cooperation is predicted to take place preferentially between members of the philopatric sex and, among the latter, between the most closely related individuals. I argue that this view of kinship is too simple and in some ways reminiscent of our early conception of the unitary role of social dominance in the patterning of primate social structures. My aim is to contribute to a more balanced view of nepotism, first by pointing out that not all categories of cooperative activities should be kin-biased. The relative importance of kinship depends

on the nature of the task to be performed and on the value of close kin as social partners in each context. Second, both the relative importance of nepotism and the extent of kin recognition and kin discrimination may be expected to vary across groups and species, even among those with similar social organizations and dispersal patterns. Intergroup and interspecific variation in nepotistic regimes has been little studied and for this reason is generally underestimated. To illustrate this point, I consider the role of the strength of within-group feeding competition as one potential factor likely to generate variation in the relative importance of nepotism and the extent of kin discrimination.

Cooperative breeding in theory and practice

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Studies of cooperative breeding in vertebrates have focused on three main questions: why helpers delay dispersal; why they do not usually breed; and why they would assist in the reproductive attempts of other group members. While it is now clear that delayed dispersal is often a response to saturated environments, answers to the second and third questions are controversial. This talk briefly reviews attempts to answer both these questions, drawing principally on studies of cooperative mammals (and meerkats, in particular). It suggests that helper breeding is typically constrained both by lack of access to unrelated partners as well as interference by dominant females and that cases where helpers breed usually represent failures by dominants to control subordinates rather than examples of adaptive reproductive 'concessions' by dominants. Most cooperative mammals occupy niches which are difficult (or impossible) to exploit without the assistance of other group members, and the second part of the talk examines the relative importance of kin selection, mutualism and coercion in maintaining helping behavior. It suggests that although all three mechanisms are important, the role of mutualism has been consistently underestimated and reviews evidence of the extensive benefits that individuals derive from living in larger groups.

Policing behavior of hamadryas unit leaders: Does peacemaking harm relationships?

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After a conflict over limited resources, friends and allies are expected to reconcile because they depend on one another for their well-being, survival, and reproductive success. Sometimes, however, third-parties intervene in conflicts in which they are dominant over and bonded to both antagonists (i.e., aggressor and victim). Such third-party interventions often stop the ongoing agonistic interaction because the

intervener protects the victim by threatening the aggressor. This policing behavior might, however, jeopardize the bond between the intervener and the aggressor, and one wonders if strategies have evolved to mitigate this possible post-conflict bond-weakening effect. Among primates, hamadryas unit leaders stand out for being very active in policing the conflicts between their females. This study explores one possible strategy whereby the unit leader males' peacemaking behavior would not harm their relationship with the aggressor females: post-conflict affiliation between interveners and aggressors (i.e., second-order reconciliation). This study uses data on within-unit conflicts among adult females collected in a colony of hamadryas baboons (*Papio hamadryas*) consisting of 11 harem-holding males and 36 females. Unit leaders were found to police about 60% of their females' fights and intervene more often on behalf of the victim than the aggressor. However, although leader males and aggressors exchanged affiliative interactions in all the post-conflict periods, the initiative was taken more often by the aggressor than by the unit leader. These preliminary results suggest that interventions by unit leaders on behalf of victim females may not weaken their bonds with the aggressor females and that the affiliative interactions that take place between them may have a role in it. Other additional mechanisms which remain to be studied will also be discussed. Partly supported by project grants PB98-0773 and BS02002-00161 from the MECyD and MCyT (Spain) to F. Colmenares. A. Barajas-Abad was supported by a predoctoral Studentship from the CM (Spain).

Experiments on simple and complex social reciprocity in capuchin monkeys and chimpanzees

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Experimental studies on cooperation in nonhuman primates, which go back to work in the early 1900's by Robert Yerkes and his students, have recently gained momentum from new theories (*e.g.* kin selection, reciprocal altruism), modeling strategies (*e.g.* game theory), and observations of spontaneous cooperation in the field, such as coalition formation and group hunting. Experimental manipulations remain crucial to elucidate the proximate mechanisms of cooperation, which have received less attention than the question of how and why cooperation evolved. One cannot expect identical proximate and cognitive explanations for the predator-inspection by guppies and the power politics of chimpanzees. There probably exist different levels of reciprocity. The kind originally proposed by Robert Trivers, which involves felt obligations and active punishment of cheaters, clearly resides at the more complex end of the spectrum. Reciprocity can be based on social symmetries (i.e. individuals distribute services based on symmetrical relationship characteristics, such as preferential association or kinship), or on mental score-keeping. Even if both mechanisms result in a reciprocal distribution of services, the first mechanism is cognitively far simpler than the second. It likely explains the majority of examples of reciprocity in the animal kingdom.

We have conducted extensive research on coalitions, grooming, and food sharing in macaques, chimpanzees, and capuchin monkeys to ascertain the cognitive level at which cooperation operates. Both chimpanzees and capuchin monkeys share food, and in both species there is evidence for reciprocal sharing. Evidence for memory-mediated reciprocity is stronger for the chimpanzee, however, especially in a study in which we compared the exchange of grooming for food. Recent experimental work with capuchin monkeys utilizes a bar-pulling task requiring one member of a pair to help the other to obtain food. The monkeys do cooperate and increase their sharing after having received the other's assistance. We also found capuchins to be sensitive to reward distribution: they take the predicted distribution into account before embarking on cooperation. And not unlike the human "sense of fairness", they reject attractive rewards if their partners receive even better ones.

Salivary cortisol and androgen in (female) bonobos: Effects of sex, status and stress

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Sexual contact may play an important role in the relationships between female bonobos (*Pan paniscus*) with rank-related asymmetries affecting frequency, initiation and duration of its expression. In spite of its frequency, the benefits the participants gain from this kind of contact remain unclear. For this reason we postulated that Genital-Genital-rubbing could be used in conflict or stress situations as a mediator of the endocrine stress response. We predicted differences in both tonic and stress response of adrenal activity (cortisol) to be associated with dominance rank. To test this hypothesis, we examined the expression of rubbing as a possible correlate of these differences. The study was carried out with a group of captive bonobos in Frankfurt zoo. Behavioral data were combined with saliva samples, which were collected for hormone analyses in the mornings (post-observation) and in the afternoons (pre- and post-observation). Baseline levels of cortisol and testosterone were compared to levels in initiated stressful situations.

Female coalitions in hamadryas baboons

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Hamadryas baboons (*Papio hamadryas hamadryas*) have a patrilineal multilevel social organization in which the one-male unit (OMU) is the smallest subgroup. Females are thought to have individualistic egalitarian dominance relationships and poorly developed affiliative networks because of low levels of within- and between-group contest competition. However, hamadryas baboons have a flexible social structure: when contest competition occurs in captivity, stable linear dominance

hierarchies and highly differentiated affiliative networks can be developed as predicted by the socioecological model. However, female coalitions are rarely or never observed, which has been attributed to the policing behavior of males that regularly intervene in female conflicts. In Antwerp Zoo, female coalitions became more frequent after a change in group composition. These coalitions are investigated in relation to age, kinship and OMU members and implications for the socio-ecology of hamadryas baboons are discussed.

The family insurance: Cooperative breeding in wild gray mouse lemurs (*Microcebus murinus*)

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Lactation imposes substantial physiological costs on mothers and should therefore not be directed towards foreign offspring. Allonursing, however, is not uncommon in species that share roosts or breed communally. Hypotheses to explain this phenomenon include brood parasitism, reciprocity and kin selection. For only a fraction of the communally breeding species, however, information on behavioral details in combination with data on kinship and kin recognition are available to identify cooperation and to distinguish among these explanations. Here we present the first report on cooperative breeding in a nocturnal primate, the gray mouse lemur. Females of this solitary species form daytime sleeping groups and give birth to 1-3 young. To determine whether females in a sleeping group are related and cooperate in infant rearing, we observed 170 individually-marked animals over three consecutive annual breeding seasons in western Madagascar. Five breeding groups of 2-3 females were filmed inside their nests with IR-video for a total of 410h during one breeding season. Tissue samples of all animals were taken to determine genetic relationships among all members of the population via microsatellite analyses of extracted DNA. We found that sleeping and breeding groups consisted of closely-related females ($0.125<r<0.5$). All females within a breeding group gave birth and regularly groomed offspring other than their own. Allonursing could be regularly filmed in three groups. However, females carried only their own offspring between nest sites, demonstrating their discrimination ability. Furthermore, in two groups, females successfully adopted young of relatives, which had died before weaning their offspring. Thus, kin selection on communally nesting closely-related females may explain the evolution of cooperative breeding in this species.

Cooperation and competition in two forest monkeys

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Seven monkey species occur at very high densities in the primary rainforest of the Taï National Park (Ivory Coast). These high densities are thought to result from niche separation in which each species only exploits a sub-segment of the available resources. Niche separation decreases interspecific competition and enables coexistence of closely related species. Although widely accepted, this explanation is insufficient to explain the occurrence of an eighth Taï monkey species, the putty-nosed monkey (*Cercopithecus nictitans stampflii*). In comparison to the other seven species, putty-nosed monkeys occur at a curiously low density in the Taï forest, although the species is relatively common in the more northern transition zones between rainforest and savannah. We conducted a 24-month field study in the Taï NP and found that intense feeding competition with one of the resident primates, the Diana monkeys (*C. diana diana*), kept putty-nosed monkeys from successfully colonizing the rainforest habitat. We assessed interspecific competition by using measures of niche overlap and by comparing the groups' occupied niches alone or in association. However, contrary to the interspecies competition hypothesis, groups of both species used almost completely overlapping home ranges and formed mixed species associations on an almost permanent basis, rather than avoiding each other. We hypothesized that Diana monkeys tolerated immigrating putty-nosed monkeys and formed mixed-species groups with them, despite high levels of competition, because of their merit in predation defence. Direct observations and a series of field playback experiments confirmed that putty-nosed monkeys played a vital role in defence against crowned eagles. These findings suggested that putty-nosed monkeys obtained access to feeding trees by offering anti-predation benefits to Diana monkeys. We discuss these findings in light of current biological market theory.

Cooperation between resident males and mothers prevents infanticide in sooty mangabeys

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In multi-male species infanticide is thought to be unlikely because a potentially infanticidal male bears all the costs, but doesn't necessarily reap the benefits. The observation of aggression directed at mother-infant pairs and unattended infants in sooty mangabeys, was therefore unexpected, while groups of this species contain large numbers of adult males. We studied patterns of male aggression and female counter-strategies in a group of around 120 animals in the Taï National Park, Ivory Coast. Data were collected on 35 adult females over a period of 10 months, including

both a mating and a birth season. Non-resident males frequently enter the study group prior to and during mating seasons (see abstract Benneton & Noë) and attempt to mate with sexually receptive females. These non-resident males attacked mother-infant pairs significantly more often than resident males. In turn, aggressed mothers counter-attacked, alone or in coalition with other females or mothers. This is in stark contrast to their lack of reaction to aggression by resident males. Furthermore, the putative fathers strongly supported both the infants and their mothers. These protector males and the mother-infant pairs remained in close proximity throughout the period of infant vulnerability. Mothers with vulnerable infants avoided non-resident and other resident males during this time. Despite 136 observed attacks on mother-infant pairs and unattended infants by non-resident males, only one infant died and its mother sustained injuries. We didn't observe the cause, however. We conclude that the cooperation between putative fathers and females with infants represents an efficient protection against infanticide.

The economics of human cooperation

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I will provide evidence challenging the self-interest assumption that dominates economics and the behavioral sciences. I will focus on three issues. First, the evidence indicates that many people have a tendency to voluntarily cooperate, if treated fairly, and to punish non-cooperators. I call this "altruistic punishment" and show empirically that it can lead to almost universal cooperation in circumstances in which purely self-interested behavior would cause a complete breakdown of cooperation. Second, I show that altruistic rewarding exists as well; it raises cooperation, but is less effective than punishment. Third, using data from a large-scale study conducted in Russia, Belorussia, Germany and Switzerland I show that norms of cooperation may strongly differ between societies.

Post-agonistic affiliative behavior between victims and bonded partners in peer-reared rhesus macaques

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A suggested function of post-agonistic affiliative behavior is the reduction of the victim's stress caused by conflict. I therefore hypothesized that victims would attempt to or make affliliative contact with their bonded partners, following a conflict. I observed 20 adult peer-reared rhesus macaques (*Macaca mulatta*), performing instantaneous scans to determine bonded partners. Focal observations were conducted on the victim of conflict for 10 minutes, utilizing the PC/MC method. Affi-

liative behavior was recorded as well as avoid, leave proximity, and follow. There was neither selective attraction to the bonded partners ($z = -1.01$, $p > 0.05$), nor was there selective attraction to the non-bonded partners ($z = 1.01$, $p > 0.05$), following a conflict. There were significantly more attracted pairs than dispersed pairs ($z = 4.098$, $p < 0.01$), but not significantly more bonded attracted pairs than non-bonded attracted pairs ($z = 0.762$, $p > 0.05$). Leaves by bonded partners were not significantly more frequent than leaves by non-bonded partners in the PC period ($z = 1.20$, $p > 0.05$), nor were there more leaves by bonded partners in the PC period compared to the MC period ($z = 1.81$, $p > 0.05$). Although I did not find that victims are attempting to make or making affiliative contact with bonded partners following a conflict, I did show that reconciliation does occur in a rhesus macaque group not bonded by kinship. Perhaps post-agonistic affiliative behavior between the victim and their bonded partners is affected by other factors, such as dominance rank, not controlled for in this analysis.

Children's economic negotiations in ultimatum and dictator games

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Recently there has been little interest in fairness as just distribution in cognitive developmental psychology. In contra-distinction, in experimental economics the sharing of resources has become a predominant experimental paradigm to analyze fairness motivation in persons and to reject the notion of economic man (FEHR, 1998). This research, however, has been predominantly interested in adults. In this study, we want to connect experimental game theory in economics with social-cognitive developmental theories. Children from grades 6 and 8 played two economic games (ultimatum and dictator game). They stated their individual preferences and negotiated the final resource sharing in a group of three. The results revealed significant effects for the type of game and age. Children, similar to adults, act strategically and offer less in dictator than in ultimatum games. However, participants in this study offered more in both games than what was expected from previous research with adults. Video-taped group discussions will be analyzed for fairness reasons and perspective-taking.

Evolutionary family conflict resolution and genomic imprinting

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Competition between siblings in the same litter over maternal resource allocation is widespread among mammals. For instance, in mice, young may compete for access to more productive teats. Who in a family decides how this conflict between

siblings is resolved: Father, mother or offspring? Parents may disagree over the extent of their offspring's competitiveness, in particular when females have to pay the costs of providing resources. This suggests that parent-of-origin-specific effects may play a role in sibling conflict resolution, but this issue has not been explored. Here, I present a first step of an analysis of parent-of-origin-specific effects in sibling competition by investigating the factors that influence offspring growth in mixed litters before weaning. Pups of a reciprocal cross between B6 and CBA mouse strains were fostered in mixed litters that consisted of half their natural siblings (e.g. B6CBA) and half the other reciprocal cross (e.g. CBAB6). Analysis of the factors that influence weight gain from birth to day 15 across half litters showed that body mass at birth is the main predictor, whereas foster mother strain had no effect. Smaller pups gained proportionally more weight than their larger littermates, after controlling for proportion of males in the litter, litter size and weight of foster mother's litter and body mass of foster mother. The same effect was found when looking at the difference in body mass increase between the half litters. However, the difference in body mass increase between half litters was also significantly affected by foster mother strain. B6CBA pups gained proportionally more mass when fostered by their own mother and vice versa, which suggests that kin discrimination within litters by females may be possible and that females adjust their provisioning accordingly.

Evolutionary game theory: Why is reciprocity so rare in social animals?

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After three decades of worldwide research on reciprocal altruism and related phenomena, no more than a modest number of animal examples have been identified. Even in primates, evidence for reciprocity is surprisingly scarce. In contrast to the shortage of support, reciprocal altruism and Tit-for-Tat-like behavior have been used as the prime explanation for cooperation among nonkin. From models based on this line of reasoning, one easily gets the impression that reciprocity should be widespread among social animals. Why is there such a discrepancy between theory and facts? A look at the best-known examples of reciprocity shows that simple models of repeated games do not properly reflect the natural circumstances under which evolution takes place. Most repeated animal interactions do not even correspond to repeated games. Partner switching and mobility often counteract the evolutionary stability of reciprocal altruism. Moreover, if learning is involved in mental implementation, then the timescale in which reciprocity can occur is often dramatically shortened. In the few known examples, quick reciprocation seems to be the rule, yet standard game theory fails to account for this empirical finding. More generally, it must be emphasized that mental mechanisms shape the evolution of reciprocity. An impressive mental machinery is required for nontrivial examples of reciprocity, as illustrated by the attribution problem (i.e., the problem of classifying other individuals' actions as cooperative, intentionally uncooperative, or unintentionally uncoop-

erative). Emotions may play a role in the machinery underlying cooperation, but current game theory is conceptually not designed to account for the role emotions play. Collectively, this shows that many obstacles can impede the evolution o reciprocity and that evolutionary game theory needs new conceptual tools to understand these obstacles adequately.

Applying socioecological models of primate coalition formation to human females

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The degree to which females form alliances and coalitions to aggress against competitors varies considerably among non-human primate species. Socioecological models of primate social organization have been useful in explaining this variation in terms of resource competition. We apply this model to the evolution of coalitionary behavior in human females. Empirical and theoretical work suggests that reputation was an important mediator of access to valuable and monopolizable social and material resources in ancestral human environments. The manipulation of reputations by the strategic collection, analysis, and dissemination of information about the actions and capabilities of group members (i.e., gossiping) may have been one way to compete for such contested resources. Over evolutionary time, women may have experienced more within-group competition than men, and female reputations may have been more vulnerable than male reputations to gossip. Consequently, gossiping may have been a more important strategy for women than men. Recent evidence strongly suggests that women compete with other women using non-physical forms of aggression like gossip. Using experimental and survey data, we explore the hypothesis that *coalitions* facilitate the ability to strategically manipulate reputations with gossip, a phenomenon we refer to as informational warfare.

Cooperation and competition in callitrichid societies – a review in light of new field data

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Societies of marmosets and tamarins – New World primates of the family Callitrichidae – are characterized by a dialectic relationship between cooperation and competition. Cooperation is manifested in communal infant care, where all group members, but particularly adult males, care for the heavy twin offspring through carrying and food sharing. At the level of social structure, this cooperative system is characterized by very low frequencies of agonistic behavior. Nevertheless, there is a high level of reproductive competition between females, which is apparent in the ha-

bitual monopolization of breeding by a single female per group, even if other mature females are present. The emergence of first genetic field data on from studies of common marmosets (NIEVERGELT et al. 2000, Int. J. Primatol. 21: 1-20) and moustached tamarins (see HUCK *et al*., abstract) provide the opportunity to examine cooperation and competition in the light of genetic relationships. Also, the non-invasive monitoring of the reproductive physiology of wild callitrichids allows re-examination of previously suggested mechanisms of single female breeding. It is hypothesized that the dialectics between cooperation and competition provide a complex social environment, in which the combination of different factors (e.g. group composition, age, genetic relatedness) requires highly variable individual behavioral strategies. This flexibility may account for the unusual flexibility of callitrichid mating systems.

Anticipation of conflict, biological markets and feeding times in zoos

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A number of studies of captive primates have noted an increase in allogrooming activity prior to predictable feeding times. These increases in grooming levels have been interpreted as a means of maintaining close social bonds in anticipation of contest competition over a clumped and predictable food source. Recently, studies of primate grooming behavior have adopted a biological market approach where grooming is viewed as a commodity that may be traded for itself or other services. One suggested service resulting from this interchange grooming is in 'buying' tolerance at feeding sites. The captive environment provides the perfect situation within which to examine this hypothesis. Here we present data from two species of primate, the lion-tailed macaque (*Macaca silenus*) and the Javan langur (*Trachypithecus auratus*) at Bristol Zoo Gardens to determine whether biological markets operate in the anticipation of conflict, or whether elevated grooming levels prior to feeding represent displacement activities resulting from elevated stress due to predictable feeding times. The relevance of the biological market approach in relation to the anticipation of conflict in primates will be discussed.

Genetic relationship in groups of a cooperatively breeding primate

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Cooperative breeding is rare in mammals, but consistently found in the New World primate family Callitrichidae (marmosets and tamarins). Due to the scarcity

of genetic studies of wild callitrichids, it is not known whether this cooperation is based on kin selection or on other benefits. We therefore studied genetic relatedness in wild groups of moustached tamarins (*Saguinus mystax*). These tamarins live in groups of 1-4 adult males and 1-3 adult females and show a polyandrous mating system, with reproduction usually being confined to a single female per group. We used 12 microsatellite loci of DNA extracted from faecal samples collected from two major study groups and six neighboring groups at the Estación Biológica Quebrada Blanco, north-eastern Peru, for genetic analyses. Relatedness between individuals within groups was significantly higher than between members of different groups, though both unrelated males and females (apart from mating partners, which were never related) occurred within groups. Thus, the cooperative breeding system of *S. mystax* may be partially based on kin selection, but other benefits have to play a role as well.

Information transfer in female Bechstein's bats (*Myotis bechsteinii*)

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Coloniality in birds and bats has been explained by the argument that communal roosts serve as information centers where colony members transfer knowledge about their habitat. I tested whether female Bechstein's bats (*Myotis bechsteinii*) living together in a breeding colony exchange information about foraging areas and roosts. I used radio-telemetry to study the nightly habitat use of adult female Bechstein's bats. Over several nights, each bat re-visited the same foraging area, although females regularly switched day-roosts at the same time. Most individual foraging areas showed no, or only little, overlap with each other. Genetic relatedness among colony members was significantly positively correlated with the degree of overlap among individual areas. Mothers shared foraging areas with their daughters. Thus, daughters may learn from their mothers where to hunt. Five females were repeatedly radio-tracked at different seasons, months apart. Even between years, all bats maintained their individual hunting areas. Because females are very loyal to their individual foraging areas and, with the exception of mother-daughter pairs, foraging areas are typically substantial distances from each other, information transfer about feeding sites is unlikely to be the crucial factor promoting coloniality. In a field experiment, I offered female Bechstein's bats, which were individually marked with implanted transponders (PIT-tags), suitable versus unsuitable roosts, which were constantly monitored with transponder readers. The arrival pattern of individual bats revealed that colony members exchange information about novel roosts among each other. Information transfer was not influenced by the degree of relatedness among colony members. In conclusion, one way female Bechstein's bats cooperate with colony members and profit from sociality is via information transfer about potential roosts. Supported by the German Science Foundation (DFG) and the Swiss National Fond (SNF).

Inter-specific communication serves to improve predator avoidance in mixed-species associations of tamarins

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Predation risk is considered to be a selective pressure for the formation of mixed-species troops by South American tamarin monkeys of the genus *Saguinus*. Participants in mixed-species troops may benefit from shared vigilance towards different types of predators or from a higher number of vigilant individuals. Inter-specific communication should play a crucial role in the realization of these benefits. To investigate this role, we studied three wild mixed-species groups of saddleback (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins. We conducted playback experiments to examine whether alarm calls are mutually recognized and presented predator models to examine species differences in predator detection. Focal animal samples were taken to establish scanning rates for the analysis of species-specific vigilance patterns. Both species distinguished their own aerial and terrestrial alarm calls, as well as the alarm calls of the associated species. The playbacks were answered with the predator-specific reactions, independently of whether the presented alarm calls were from conspecific or heterospecific individuals. In contrast to the hypothesis, vigilance was not shared according to the characteristic height division of the species: the lower-ranging saddleback tamarins looked significantly more upwards, and the higher- ranging moustached tamarins looked significantly more downwards. No evidence for a better detection of terrestrial predators by saddleback tamarins was found. Both species decreased scanning rates with a higher number of conspecific group members within close proximity of the focal animal, but did not decrease scanning rates with closer proximity of heterospecific group members to the focal animal. In contrast to findings of PERES (1993, Folia Primatol 61: 61-76) height-specific sharing of vigilance seems to be of minor relevance in mixed-species associations of *S. fuscicollis* and *S. mystax*. However, our results indicate that tamarins reduce predation risk by inter-specific communication.

Cooperative breeding in mammals

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Many mammalian societies can be understood as extended families centered around cooperative breeding. Such cooperative care of alien young has been described both for non-breeding and breeding females, and provisioning of care to non-offspring in such societies can be facultative or obligatory. I will review the types of non-offspring care that are known from mammals, and the actual and potential fitness benefits and costs for the donor and recipient of such behavior. I will use

our own work on house mice to further focus on indiscriminant non-offspring nursing among breeding females in egalitarian groups. Although not widespread, non-offspring nursing is more common among breeding than non-breeding females, which may be due to higher costs of lactation than those of other types of parental care.

Sex differences in sociality

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Sex differences in sociality have often been reported and are usually attributed to dispersal patterns and the advantage of kin relationships. Thus, the finding that male East African chimpanzees show a high degree of sociality and affiliative behavior, whereas females are generally solitary has been attributed to the fact that females disperse while males are philopatric. However, recent studies have shown that on average chimpanzee males within a community are not more closely related than are females. Furthermore, observations in West Africa have long suggested that females also show high degrees of affiliative behavior. We investigated, using up to 10 years of behavioral data, whether the chimpanzees of the Taï Forest (Côte d'Ivoire) exhibit sex differences in three social parameters: dyadic association, party composition and grooming interactions. We found a significant sex difference in all three parameters, i.e., males had higher mean dyadic association indices (DAI), spent less time alone and groomed more and for longer periods than females. However, females had DAIs comparable with mixed-sex dyads, spent only a maximum of 18% of their time alone or with their offspring and spent a considerable amount of time grooming each other. Furthermore, maximum values of DAIs found in females did not differ from those found for males, indicating that females have similarly close associates within the community. These findings are in contrast to reports on female East African chimpanzees, which spend most of their time alone and rarely engage in female-female grooming interactions. These results suggest that both male and female chimpanzees show a high degree of sociality and that current models about the evolution of sociality have to integrate the possibility of pronounced female sociality in a male philopatric system.

Reproductive competition does not mean physiological suppression in wild female tamarins

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In marmosets and tamarins (Callitrichidae), reproductive competition between females is strong and breeding usually restricted to a single female per group. Captive studies have suggested that reproductive monopolization by the breeding female is mediated through physiological suppression of ovarian activity in other adult females and/or interference of their sexual interactions. In order to examine whether non-breeding females in wild tamarin groups also show ovarian inactivity, we monitored the reproductive status of breeding (n = 2) and non-breeding females (n = 2) in two groups of moustached tamarins (*Saguinus mystax*) at the Estación Biológica Quebrada Blanco in Peruvian Amazonia. Profiles of immunoreactive pregnanediol glucuronide (PdG) and total estrogens (E) were generated from fecal samples collected throughout a one-year period. Non-breeding females showed clear signs of ovarian activity, as indicated by hormone concentrations and a temporal pattern in progestogen and estrogen excretion, which were essentially similar to those recorded for the breeding females (outside the latters' pregnancy and period of post-partum ovarian inactivity). Thus, reproductive monopolization in female *S. mystax* is not generally mediated through the suppression of ovarian activity in non-breeding group members. Rather, we hypothesize that the presence or lack of ovarian activity in non-breeding females is part of their reproductive strategies, which are influenced by factors such as age and group composition.

Food-sharing in common marmosets (*Callithrix jacchus*): An experimental approach in a captive setting

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Food-sharing is a widespread phenomenon in the taxon Callitrichidae. There are reports of food-sharing in wild callitrichid species but the abundant literature stems from descriptive studies in captivity. In assuming the most likely evolutionary scenario, food-sharing must have evolved in habitats with relatively dense vegetation, i.e. where members of a dispersed foraging group are often hidden from sight of the others. In this setting, specific "food calls" are likely to evolve because they alert and direct infants to a food possessor. There are three obstacles for the analysis of food-sharing in captivity: (1) Food transfers elapse very rapidly. (2) Cages are restricted in space and often poorly structured, i.e. members of a group are in permanent visual contact. (3) Infants react to feeding noises and quickly rush to a food pos-

sessor, i.e. food transfers may not have been initiated by food calls of the donor. Therefore, regardless of how carefully conducted, observational descriptive studies do mostly not allow to distinguish unequivocally between passive (in sensu "tolerated theft" or "response to begging") or active (in sensu "food offering") sharing. We approached the phenomenon experimentally because it allowed us to discriminate between the two forms of food-sharing, which must result from differences of the underlying motivation of the donor animal.

The rationale for the experiments was to make food transfers impossible for a while, i.e. to separate the food possessor from the potential recipient by an opaque screen. In all trials the food was crickets, which are highly prized. Six pairs of first-time marmoset parents plus their twin offspring served as subjects. (1) If undisturbed families are provided with the same number of crickets as there are group-members, mothers consume significantly more crickets than both fathers and offspring do (36 replicates per family between week 6 and 12 after the infant's birth). (2) Singly separated parent individuals emit food calls after receiving a cricket but do consume it at the same time, i.e. there is no indication that the highly-prized food is "saved" for the infants. Fathers did significantly more food calling than mothers did (70 replicates per individual between week 6 and 12 after the infant's birth). (3) If parents are separated as pairs and each individual alternately receives a cricket there is food calling but no food-sharing between the adults, i.e. food calling is directed towards the out-of-sight infants (50 replicates per dyad between week 8 and 12 after the infant's birth). (4) If a parent is separated together with an infant and receives a cricket, the cricket is transferred to the infant. Fathers transfer food in all cases, mothers do so to a lesser extent, but there was no significant difference between the sexes (50 replicates per dyad between week 8 and 12 after the infant's birth). Thus, there is active food-sharing in common marmosets, i.e. uni-directional from parents to infants. There is a tendency that mothers share less food than fathers do. This can be explained by the pronounced asymmetry between the sexes with regard to reproductive biology, i.e. twinning and a new conception during the lactation period puts a disproportionately heavy physiological and physical burden on the female.

Reputation, personal identity and cooperation in a social dilemma

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The problem of sustaining a public resource that everybody is free to overuse emerges in many social dilemmas. Public goods experiments usually confirm that the collective benefit will not be produced. Because individuals and countries often participate in several social games simultaneously, the interaction of these games may provide a sophisticated way by which to maintain the public resource. Indirect reciprocity, `give and you shall receive', is built on reputation and can sustain a high level of cooperation. We show, through alternating rounds of public goods and indirect reciprocity games that the need to maintain reputation for indirect reciprocity

maintains contributions to the public good at an unexpectedly high level and leads to high profits for all players. Reputation may be a currency that is valid in many social games if individual identities are transitive. However, human subjects use different strategies conditional on being anonymous or recognizable. Being recognized as the same individual in both scenarios motivates players to invest in their reputation and thus in sustaining the public resource. Cooperation declines if individuals have different identities in the two interacting games. To dissect the mechanism of the interaction between the public goods and the indirect reciprocity game further, we tested whether building a good reputation in public goods games is not only valuable within the own social group but also in a new group. As expected, members of the same social group responded strongly in the indirect reciprocity round to the reputation gained in the preceding public goods round. However, also members of other groups rewarded an individual's good reputation from preceding public goods rounds in indirect reciprocity rounds. This shows that players may sustain the public resource in order to profit in future encounters with others in and outside their own social group.

Reciprocal exchange in chimpanzees and other primates

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Reciprocal exchange is an integral part of cooperative behavior in humans. Studies of an unusually large community of chimpanzees at Ngogo, Kibale National Park, Uganda, suggest that such exchanges occur commonly in this species as well. At Ngogo, social bonds between male chimpanzees appear to be based on reciprocal exchanges made in several different currencies. In this paper, I review observations that indicate male chimpanzees trade services in the contexts of grooming, coalition formation, meat sharing, and territorial boundary patrols. I compare these findings with those from other anthropoid primates and consider the processes that might account for the evolution of reciprocal exchange in wild chimpanzees.

Effects of the size of the enclosure on the weight loss after the birth of infants in cotton-top tamarins (*Saguinus oedipus*)

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Offspring birth in captivity in the cotton-top tamarin (*Saguinus oedipus*) has consequences for group members, which are reflected by weight losses. It has been suggested that such weight losses should be even higher in the wild, where individuals have to cope with longer travel distances. In this study, average weight losses during the first 9 weeks after birth were compared among individuals from 8 cotton-top

tamarin groups. Four groups were housed in big enclosures (43 m^2 and 3,3 m high) and four in small enclosures (12 m^2 and 2,4 m high). A two-tailed Mann-Whitney U Test was used for the analysis, with a $p < 0,05$ significance level. Results indicate that adult males ($p < 0.01$) and adult females ($p < 0.01$) housed in big enclosures lost more weight than individuals from enclosures with a smaller size. Male and female subadults together also tended to exhibit greater weight loss in big enclosures ($p = 0,15$). Mothers' body weight, in contrast, was not affected by the size of the enclosure ($p = 0,77$). Thus, whereas body weight of those individuals that cooperate in offspring rearing is affected by the size of the living area, this aspect does not seem to be important for subadults and reproductive females in large groups. Financial support: MC y T DGI PB98-0094; MC y T DGI BS02002-02611.

The roots of economic behavior

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The trading of commodities like goods, services and information between human beings is almost certainly the most widespread form of cooperation between unrelated members of the same species on earth. Trading would not take place if it would not normally result in a net benefit for all participants, but the potential for conflict over exchange rates looms large. It is therefore crucial for each trader to have a number of mechanisms at his disposal that ensure optimal profit. I will speculate about the evolutionary roots of such mechanisms. I will only consider 'simple' trade, i.e. direct transactions between individuals without binding contracts. It is also typical for humans to contribute to and rely on institutions that ensure fair trade by enforcing contracts, such as police forces, justice systems and religions, but these are beyond my scope. The most important sets of mechanisms can be bracketed together as 'partner choice' and 'partner control'. The possibility of partner choice and thus partner switching is what makes markets turn: it ensures the link between supply-demand ratios and exchange rates of commodities. Partner control becomes important only after trading relationships have formed: it ensures continuing profit from ongoing relationships.

I will concentrate on partner choice. It is obvious that one can search among naturally occurring cases of cooperation and mutualism for the roots of relevant mechanisms. i.e. those interactions Peter Hammerstein and I baptized 'biological markets'. However, one should also consider mechanisms that evolved under sexual selection, while these mechanisms were in place long before the cognitive mechanisms relevant to cooperation and trade emerged. Sexual reproduction is *de facto* a form of cooperation and mates are chosen on 'mating markets'. We should not only work backwards from mechanisms humans use to select their mates, however, but also look at related strategies used to select same-sex friends. That way we should be able to identify homologous mechanisms in non-human primates and also further out on the phylogenetic tree.

Indirect reciprocity and the evolution of social norms

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Humans are unique in the degree to which they possess and use culture. Although there is a growing body of theoretical work on the evolution of culture, the existence of social norms is still somewhat of a puzzle. Particularly vexing are those norms which are costly to the individual performing them, while beneficial to the group (i.e. public goods). How can selection favor such altruism? Recent theoretical accounts typically invoke (1) costly signaling or (2) punishment coupled with (cultural) group selection. At the same time, a growing body of research has explored indirect reciprocity, wherein selection favors strategies that cooperate with those that are cooperative. In this paper we show that when social norms and indirect reciprocity are coupled, such that being a good citizen involves participation in the social norms, selection can stabilize normative behavior, even if it is costly to the individual. As in other models, selection is often ambivalent as to what norm is favored; those that are maladaptive are often as likely to emerge as those that are group beneficial.

The influence of food shareability and competition on the cooperative problem-solving behavior of chimpanzees (*Pan troglodytes*)

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Chimpanzees in the wild have been observed to cooperate when forming coalitions and in the context of hunting. However, the few experimental studies that have investigated their cooperative problem-solving abilities have shown that even in experiments in which the task itself was intuitive, like pulling a rope attached to a baited box, their cooperative behavior was far from spontaneous. Possible explanations for these findings are that the tasks did not offer enough motivational incentives to elicit cooperation, or that social constraints, such as tolerance levels between the subjects, limited their possibility to work together. The first goal of this study was to find a context, in which chimpanzees cooperate spontaneously and without training. Further, we investigated how tolerance levels between chimpanzees influence their cooperative behavior in an instrumental task. We manipulated two variables in order to increase or decrease the inter-individual tolerance: i) the opportunity to monopolize a food-reward and ii) the presence or absence of a common competitor. We chose 6 tolerant dyads (N = 12) and presented them with an intuitive pulling task consisting of 2 ropes attached to a baited tray. The distance between the ropes required the two individuals to pull the ropes separately but simultaneously. Subjects were confronted with the following conditions: i) distributed and highly

sharable food versus clumped and easily monopolizable food, and ii) a social-competitive pulling task versus a simple pulling task. In the competitive condition subjects competed against another chimpanzee dyad, who pulled in the opposite direction from the other side of the baited tray. Our hypothesis was that both the presence of highly sharable food and the social-competitive context would increase their tolerance level and motivation to work together in order to defeat the competitors. We discuss the results in terms of the constraints that tolerance, costs, and pay-off structures may have on chimpanzee cooperative behavior.

Cooperation through interdependence

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Existing theories of cooperation can explain helping among relatives or reciprocating pairs, but it is increasingly being recognized that many behaviors cannot be explained in these terms. Here we show how cooperation is readily established in groups without reciprocity or kinship. We consider a simple two-stage scenario in which individuals first have an option to help others at the expense of their own fitness, and are then subjected to a predation process in which their chances of survival increase with group size. We find that although altruism cannot be favored when we consider the helping stage alone, it is readily established when we add in the group-size dependent process. We explain this in terms of a feedback effect whereby helping others benefits the altruist secondarily. This can be formalized in terms of the 'stake' of one individual in another, where the stake is a measure of the extent to which the altruist's own fitness increases with that of its beneficiary. We argue that such interdependence between individuals is a widespread and important factor promoting cooperative behavior.

Third-party affiliation and stress-related behaviors of aggressors in baboons (*Papio hamadryas hamadryas*)

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In the aftermath of aggressive conflicts, former opponents can engage in several types of interactions. Third-party affiliation has been defined as any affiliative interaction between opponents and other group members. Most studies of post-conflict third-party affiliation have been carried out in macaques and have been mainly concerned with reporting its occurrence/absence; few attempts have been done, however, at investigating its possible functions. It has been suggested, for example, that post-conflict third-party affiliation might reduce the probability of receiving further

attacks (from the other opponent and/or from a third-party), be used for recruiting support, serve to appease potential hostile interveners, reinforce the dominance hierarchy, and reduce the individual's levels of stress. In this study, we investigate the occurrence of post-conflict third-party affiliation initiated by aggressors in a colony of hamadryas baboons (*P. h. hamadryas*) and test the hypothesis that one of the functions of aggressor-initiated third-party affiliation is to reduce the aggressor's levels of post-conflict anxiety. We did focal sampling of aggressors and collected 648 10-min post-conflict (PC) samples and the corresponding matched control (MC) samples in which we recorded all aggressive and affiliative behaviors between opponents and third-parties, and we use self-directed behaviors (SDBs) as indicators of anxiety (MAESTRIPIERI et al. 1992). After a conflict, aggressors directed more affiliative contacts to third parties than in control periods. Aggressors also showed increased rates of SDBs during the first minutes of the PC period. However, we did not find evidence in support of the hypothesis that third-party affiliation serves to reduce the aggressor's levels of anxiety as the rates of SDBs did not decline when aggressors affiliated with third parties. Post-conflict third-party affiliation initiated by aggressors (and victims) is likely to have multiple functions, including the reduction of the individual's levels of stress. However, these functions might vary according to the type of affiliative behaviors exchanged and the relationship characteristics between the incumbent individuals. Future studies should focus on finer-grained analyses, which allow to establish the relation between these variables and the possible functions of third-party affiliation initiated by aggressors (and victims).

Volunteering leads to rock-paper-scissors dynamics as an escape from human social dilemmas

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Collective efforts are a trademark of both insect and human societies. They are achieved through relatedness in the former and through largely unknown mechanisms in the latter. The problem of achieving cooperation among non-kin has been described as the 'tragedy of the commons' prophesying the inescapable collapse of many human enterprises. In public goods experiments, initial cooperation usually drops quickly to almost zero. It can be maintained by either the opportunity to punish defectors or the need to maintain good reputation. Both scenarios require defectors being identified. Recently, theorists proposed a simple but effective mechanism operating under full anonymity. With optional participation in the public goods game "loners", i.e. those players who do not join the group, defectors and cooperators will coexist through a rock-paper-scissors dynamics. We showed experimentally that volunteering easily generates this dynamics in public goods games and that manipulating initial conditions can produce each predicted direction – if defectors are pretended to predominate, loners soon become most frequent, as do cooperators after loners and defectors after cooperators, respectively. On average cooperation is perpetuated at a substantial level.

Practicing Hamilton's rule: Patterns of cooperation in primate groups

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Evolutionary theory tells us that altruism can evolve through kin selection or reciprocity. In animal groups, there are numerous examples of nepotism, which are thought to be the product of kin selection, but relatively few examples of cooperation among non-relatives that could be the product of reciprocity. In fact, new evidence of paternal kin recognition in primate groups suggests that nepotism is even more prevalent than we had previously believed. Examples of reciprocity in primate groups are extremely uncommon, and in most cases we cannot exclude the possibility that partners are paternal kin. I will argue that nepotism is the product of kin selection, and that kin selection is the driving force underlying the evolution of cooperation in primate groups.

The selfish nature of generosity: Harassment and food sharing in primates

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Recent theory predicts that imposing costs on others via punishment can stabilize cooperation in social dilemma games. The problem faced in punishment situations is the same as that faced in cooperative situations: cheating (not punishing) is often more profitable than punishing because punishment is costly to punishers. I present harassment ('sharing-under-pressure') as an alternative that circumvents the cheating problem. When harassing, an individual imposes costs on a defector during the cooperative interaction, potentially manipulating the defector into cooperating. I tested predictions of harassment theory in a food sharing experiment using captive subjects of two primate species: squirrel monkeys (*Saimiri boliviensis*) and chimpanzees (*Pan troglodytes*). By controlling food possession and contact between a pair of subjects, I manipulated harassment potential and measured the effects of harassment on sharing. In treatments in which subjects were able to harass, they often did harass. In addition, owners shared more frequently when beggars harassed more intensely. Interestingly, squirrel monkeys and chimpanzees shared equally frequently in this experimental situation despite a much higher natural sharing rate in chimpanzees. The results suggest that the immediate benefits associated with harassment can play a significant role in primate food sharing. The selfish nature of harassment could provide a simpler alternative to punishment and reciprocity in food sharing and other cooperative contexts.

Bonding in bonobos

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Based on previous studies in captivity, bonobos have been described as a "female-bonded" species. This approach has been criticized for two reasons, however. First, it is believed that behavior of bonobos in captivity differs from wild conditions. Secondly, it may be that female bonding is a characteristic of the few captive groups that have been studied so far, but not a universal pattern of all captive groups. To address the first point, we use the "adaptive potential" approach, defined by de WAAL (1994). Secondly, we studied social behavior in five different well-established groups (Wuppertal, Apenheul and Twycross, and Planckendael at two different periods), totalling about 1900 study hours, and comprising 14 mature males and 15 mature females. We analysed data on proximity, grooming, sexual contacts and agonistic support. We used cluster analyses to inspect data visually and matrix correlation to test statistically for the effects of sex and dominance on bonding patterns. Although we did find evidence for female bonding in some characteristics in some groups, these patterns were not ubiquitous. In one group only more than one behavioral category occurred significantly more among females than among other dyads. This group was also the most recently established and contained no mother-son pairs. We suggest that in recently established groups female bonding may prevail, while intersexual bonds, including mother-son bonds, take longer to develop. Furthermore dominance may be more explanatory than gender in relation to bonding. In groups where females systematically occupy the highest–ranking positions, female bonding may occur. In groups with mixed dominance relations between males and females, female bonding need not be stronger than intersexual bonding.

Two distinct psychological mechanisms underlie strong reciprocity – experimental evidence

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In this study, I present empirical evidence that two distinct psychological mechanisms – empathy (i.e., hot-emotion) and equality (i.e., cold-decision heuristics) – are responsible for producing so-called cooperation under anonymity. In social psychology, it is known that there is a stable individual difference on human cooperation and the scale measuring that difference is a good predictor of several types of cooperative behaviors under anonymity where performance contingent-payment was used – fair offer in dictator game, reciprocation in one-shot trust game, and cooperation in public goods dilemma game. In the present study, I replicated these findings and further showed that cooperators were classified into two groups whose cooperation was driven either by empathy or equality-heuristics. I demonstrate that, in major

experimental games widely studied in economics, both groups of people act in the same way. In that sense, one may argue that it is meaningless to classify proximate mechanisms of human cooperation. However, we found that these different psychological mechanisms lead to different behaviors in some important types of social interactions, including third-party punishment game (FEHR & FISCHBACHER, 2003). I propose that examining proximate mechanisms of human cooperation is not trivial because they have different ontogenetic roots and behavioral implications.

Reciprocal altruism: An unbiased view of progress since 1971

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It was obvious that HAMILTON'S (1964) theory was unable to explain an important class of human behavior that had more to do with friendship and reciprocal relations than with kinship. In 1971, I attempted to outline the problem in a way that would make the possible domain as large as possible (e.g. between species) and, at the same time, account, in principle, for key features of human psychology. Not having had a fresh idea on the subject since then, I will attempt here an unbiased view of progress since 1971. The evidence for reciprocal altruism outside our species is viewed by some as being compelling and fairly general. Others regard it as non-existent. I belong to the former camp and have been especially impressed by semi-natural and experimental work on non-human primates, but also by selected work outside primates such as work on reciprocal egg trading in sea bass and symbioses between species. Game theory has made two very important contributions to the subject, one theoretical and one empirical. The theoretical demonstrated a core logic - in its simplest form, tit-for-tat - which was exposed when a variety of strategies were thrown into competition with each other in iterated games that mimicked reciprocal altruism. This could be explored mathematically in search of evolutionarily stable strategies, i.e. those expected to predominate over time. Likewise, the theory has been expanded to include a variety of more complex options, such as punishment, varying rewards, and so on. The empirical advance provided by game theory was to provide a mechanism for measuring human behavioral tendencies relevant to cooperation. Put people into games in which they have to make choices with real consequences, e.g. pay for the privilege of punishing others. Or make them accept or reject a one-time financial offer that is more or less biased in favor of the giver or taker. Or photograph people in the act of making such decisions and see whether others differentially remember their faces depending on the kind of choice they are making. We can only hope that this methodological advance will hasten the day in which social psychologists give up the attempt to describe and understand human behavior, using paper and pencil tests (e.g. homophobia scale). Reciprocal altruism may also occur between the two halves of the genome and heterozygous advantage provides an example. Cooperation may break down - for example, at the time of meiosis. One intriguing possibility is that reciprocal relations develop between oppositely imprinted genes. This may include reciprocal altruism between relatively paternal and maternal personalities of the same individual.

Toward a general model for within-group coalitions among male primates

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Perhaps the most common form of cooperation among primates is the formation of coalitions. In constant-sum situations, such as when males within a mixed-sex group compete over opportunities for fertilization, coalitions are not easily explained because any increase in payoff for one of the partners may produce a decrease for the other(s). We develop a model for rank-changing coalitions in such constant-sum situations. For such coalitions to occur, they must be both profitable (i.e. improve fitness) for both partners and feasible (i.e. be able to beat the targets). The model assumes that payoffs show an inverse exponential distribution with rank, and that the value of the coalition is the sum of the payoffs of the partners in their original ranks. In general, the model indicates that coalitions are feasible only when the contest among males is not too strong, and where costs of coalition formation are moderate. We predict four basic coalition types: (1) rank-changing coalitions targeting individuals ranking above all coalition partners; these are expected to involve coalition partners rank just below their target, concern top rank and be small, just 2 or 3 animals; (2) bridging coalitions, where higher-rankers support lower-rankers to rise to a rank right below them; these are only expected among relatives; (3) non-rank-changing coalitions by high-rankers against lower-ranking targets; these are expected to serve to counteract or prevent the first type; (4) non-rank-changing, leveling coalitions, where coalitions partners all rank below their target; these are expected to be large and mainly involve lower-ranking males. We review the empirical patterns found among wild primates in order to test the extent to which these predictions are met.

Philopatry, relatedness and cooperation in wild chimpanzees

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Chimpanzees and humans are two of the very few mammalian species in which males typically remain their entire lives in their natal community while females emigrate. Explanations for this unusual pattern have invoked the importance of kinship bonds in promoting affiliative and cooperative behaviors among philopatric males in social groups of these species. In order to evaluate the potential impact of kin selection on the social behavior of male chimpanzees, we used microsatellite genotype data to estimate average relatedness of male and female chimpanzees from a

total of 4 habituated communities located in West and East Africa. We found that average relatedness levels among male community members, even when subdivided into cohorts of similarly aged individuals, are very rarely significantly higher than average relatedness among community females. Furthermore, although the average relatedness of males within communities tends to be higher than between communities, this difference is not significant. In order to check the generality of these results, simulations were conducted and revealed that low average relatedness among community males is the expected outcome under realistic demographic and reproductive skew situations. These results suggest that affiliative and cooperative behavior in male chimpanzees are more likely attributable to direct benefits derived by individuals than to indirect benefits via kin selection.

Blood-sucking bugs (Reduviidae, Heteroptera): A gentle and minimal invasive method for obtaining blood from mammals in endocrinological and hematological studies

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To capture animals and to collect blood after anaesthesia is often difficult or even dangerous to animals. In case of small mammals, it may be even impossible to access blood without inducing damage to the small blood vessels. Our recent studies in some small mammals showed that bugs (*Dipetalogaster maxima*) from subtropic regions can be used to obtain blood from veins, which may be difficult or even impossible to access by human experimenters with conventional methods. Here, we summarize our current knowledge about this novel method to stimulate its application in primatology. To see whether there are differences in blood samples, which were collected either with bugs or with a conventional method, we made two experiments in domestic rabbits (*Oryctolagus cuniculus*): (1) for endocrinological studies we compared concentrations of three steroid hormones (cortisol, progesterone, testosterone) and (2) for veterinary studies we compared hematological parameters. Overall, we could not find significant differences in steroid hormone concentrations between the two methods. As domestic rabbits had lower concentrations of cortisol when bugs were used instead of conventional syringes and needles, we conclude that bugs pose less stress on the animal than the conventional method. Theoretically, bugs could also be used in animals that are not handled by an experimenter and thus it may be possible to measure baseline stress levels. We find that the bug method is superior to recently developed non-invasive techniques that involve the measurement of steroid metabolites as the latter method requires preliminary validation studies to establish which fecal metabolites predominate and which antibodies work well. Regarding the second experiment, we found that most hematological parameters did not differ between the bug and the conventional method. Summarizing, we conclude that the bug method is a gentle and minimal invasive method with a great potential for studies in primate species.

Seasonal birth rates in academic and non-academic women

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The environment can affect the distribution of the birth sex ratio (BSR) in humans. The seasonal influence on birth frequencies in humans is evident in most parts of the world. However, the findings on seasonality in human BSR are not always correlated and a number of works report a miniscule variation. Here, seasonal differences in BSR of 1,928 births from 1,202 women employed at the University of Vienna were analyzed. The anonymous data set was categorized in births of academics (N = 581) and non-academics (N = 1,347). At the time of first birth, non-academics were 4 years younger than academics. Both groups did not differ in their overall BSR. However, the seasonal course of male births in academics showed significantly increased numbers during spring and marginal differences of birth rates during the other seasons. The numbers of female births were characterized through less variation. Non-academics showed a less pronounced increase of male births during spring. Detailed analyses of SBR in single births showed no seasonal effect in both groups (values > 0.5). Academic mothers exhibited significant seasonal variation of BSR between spring and summer (first born: spring 0.5652, summer 0.2564; second born: spring 0.6956, summer 0.3571) of their first and second born offspring. In contrast, non-academics showed less BSR variation (note, all values > 0.5). The results of this study suggest that academic women increase their BSR during the springtime, perhaps by using different photoperiodic conditions more selectively than non-academics. During spring the investment in sons could be advantageous because men born in spring have increased body height and subsequently, greater reproductive success than shorter men.

With whom to communally nurse? Dynamics of communal nursing in wild house mice in a barn

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Even though communal care of young is a rather frequent phenomenon in animal societies, communal nursing, where milk is shared between own pups and young produced by another mother, is rare. The house mouse (*Mus domesticus*) is one of the few species where indiscriminant nursing of own and alien pups is known. Since lactation is energetically costly, this behavior demands an explanation. Lab experiments have pointed at the adaptive value of such communal nursing behavior. Individual females that reared their pups communally with a familiar sister, had a significantly higher lifetime reproductive success (LRS) than females rearing litters on their own or females in groups of three (KÖNIG 1994, Behav Ecol Sociobiol,

34:275-283). Individual females in pairs with familiar sister also had higher LRS than individuals in pairs of previously unfamiliar and unrelated female partners. The aim of this study is to test specific predictions derived from our lab experiments on a population of wild house mice in a barn. We expect that communal nursing influences the structure of house mouse societies.

Paternal kinship among adult female rhesus macaques

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The impact of maternal kinship on social behavior has been studied in detail in many primate species, but it is difficult to assess the importance of kin selection in shaping the evolution of social behavior when studies are limited to maternal kin, completely ignoring paternal kinship. The goal of the present study was therefore to investigate the impact of paternal kinship on social relationships among adult females in one group of rhesus macaques (*Macaca mulatta)* living on the island of Cayo Santiago. Focal observations on affiliation, aggression and coalition formation were collected from 34 adult females with respect to their maternal half-sisters, paternal half-sisters (determined via genetic paternity analyses) and unrelated females. The results confirmed that most affiliation and support, but likewise aggression, was found among maternal half-sisters. Intriguingly, adult females were significantly more affiliative with their paternal half-sisters than with non-kin. As peers are more familiar than non-peers, paternal half-sisters of the same age were more affiliative than paternal half-sisters of different age. When controlling for familiarity among age mates, females preferred their paternal half-sisters over non-kin even within their peer group. No such discrimination was found with respect to dyadic aggression, suggesting context-dependent paternal kin discrimination. In contrast to maternal half-sisters, females did not support their paternal half-sisters more often than non-kin, but tended to target them less often than non-kin. This might be due to rank difference which can be high among paternal half-sisters and non-kin respectively, but which are always low among maternal half-sisters, implying that lower-ranking females risking too much retaliation when intervening in conflicts between two higher-ranking opponents. Given that paternal sibship is frequent in other primate species too, its impact on primate social relationships was probably underestimated to date.

The choice of post-conflict interactions

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Some costs of conflicts remain after an aggressive interaction has been terminated. Post-conflict management in social living animals can reduce those costs by

means of a variety of interactions implemented after aggression (e.g. reconciliation, consolation, redirected aggression). Although each post-conflict interaction (PCI) provides different advantages and disadvantages, their functions may sometimes overlap. Individuals can therefore choose from a pool of PCIs to achieve the most favorable outcome within a given conflict situation. I examined 876 dyadic aggressive interactions among 18 wild chimpanzees (*Pan troglodytes verus*) of both sexes in the Taï National Park, Côte d'Ivoire. Taï chimpanzees were able to scoop from a pool of six different PCIs and 'no PCI'. I used multivariate analysis to investigate which conflict-condition led to which type of PCI and related the choice of PCI to its advantages and disadvantages. Taï chimpanzees used reconciliation to resolve conflicts among high value partners and when approaching the former opponent was unlikely to entail further aggression. Consolation seemed to substitute for reconciliation, when opponents were low value partners or approaching the former opponent was too risky, such as when further aggression was likely. Taï chimpanzees renewed aggression after undecided conflicts and when losers were unexpected. They used redirected aggression after long conflicts, possibly because friendly PCIs were likely to fail. However, Taï chimpanzees continued with business as usual when conflicts were very short, and they avoided further interactions when the accessibility of the resource was unlimited. Taï chimpanzees appeared to follow a clear-cut evaluation process as they seemed to weigh advantages against disadvantages for the appropriate choice of PCI.

Competition and grooming pattern in hamadryas baboons

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Social grooming is prominent among cooperative behavior in primates. Here one individual can achieve an advantage (e.g. removal of ecto-parasites or stimulation of endorphine secretion) with the help of another, which would be impossible to achieve without cooperation. At the same time, grooming creates costs for the donor while increasing the fitness of the recipient. On theoretical grounds, reciprocity of grooming it is therefore expected, or grooming should be exchanged for other commodities in the sense of biological markets. To what extent grooming is exchanged for grooming or other commodities, such as tolerance at food resources or support in agonistic encounters, should depend on dominance relationships and the prevailing competitive regime. Within dyads, investment in grooming should be higher in subordinates if food becomes more monopolizable and if dominants share access to resources. In contrast, in egalitarian species or in situations where resources are not monopolizable, grooming should be exchanged only for grooming and we should find reciprocal grooming relationships. These predictions had been confirmed in a study of female chacma baboons (*Papio ursinus*), a species living in a female-bonded, multi-male multi-female society.

In contrast to chacma baboons, hamadryas baboons (*Papio hamadryas*) are believed to be more egalitarian and, hence, we expected a higher degree of reciprocity within female grooming dyads. However, in hamadryas baboons we also expect a strong female bias in female-male grooming dyads, because hamadryas baboons live in one-male units, where the adult male is the most dominant individual in the group, and, hence, the one who controls access to resources. We analyzed grooming pattern in an experimental study with captive hamadryas baboons under normal and clumped food distributions to test these predictions. In contrast to the predictions of the biological market theory, we found only a low and similar degree of reciprocity in female - female grooming dyads under both feeding conditions. However, grooming in female-male dyads supported our prediction. In the more competitive situation (clumped food-distribution) females groomed the male more than in the relaxed situation. We conclude that the pattern of cooperation, here grooming, in hamadryas baboons is influenced by the competitive regime and by the species' social system.