



DIPLOMARBEIT

Titel der Diplomarbeit

Post-conflict Behaviour and Relationship Quality in Common Marmosets (*Callithrix jacchus*)

verfasst von

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angestrebter akademischer Grad

Magistra der Naturwissenschaften (Mag. rer. nat.)

Wien, im Mai 2013

Studienkennzahl lt. Studienblatt: A 439

Studienrichtung lt. Studienblatt: Diplomstudium Zoologie

Betreuer: Univ.-Prof. Dr. Thomas Bugnyar

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1. Acknowledgements

I am grateful to Prof. Dr. Thomas Bugnyar for giving me the opportunity to conduct this project. It is a follow-up study of a student group project in the summer term 2010, which was supervised by Dr. Orlaith Fraser. I would like to thank Orlaith for introducing me to the topic of post-conflict behaviour and its connection to relationship quality back then, as well as providing valuable comments during all stages of the current study and help with methodological and statistical questions. Many, many thanks also to my unofficial supervisor Mag. Tina Gunhold, for always being available and ready to help and for proof-reading even the earliest drafts of the thesis. Thank you for all your time and effort.

Furthermore I would like to thank Vedrana Šlipogor, whom I was lucky to share the lab with, for sharing information and ideas, motivating and sometimes providing an outside perspective. My thanks also to Miriam Sima for her Solomon Coder tutorial, as well as Niki Sahling and Rebecca Nowak for creating two excel-makros which made my life a lot easier.

Finally I would like to thank and my parents Eva Faltin and Christian Faltin for their financial support and Andreas Raab for moral support.

2. Introduction

Gregarious animals often have to deal with within-group conflicts in a number of different contexts (Aureli et al. 2002). Possible negative consequences of conflicts include stress and uncertainty about the future of the relationship, continuing tension and renewed conflict (Cords & Aureli 1996), as well as less time spent foraging due to increased social vigilance (Aureli 1992). To buffer those consequences, social mechanisms are needed to repair relationships and thus reduce post-conflict anxiety. One such mechanism has been termed “reconciliation” and is defined as a friendly interaction between former opponents soon after a fight, aiming to restore the relationship to its previous state (de Waal & van Roosmalen, 1979). Reconciliation is especially well-studied in primates [e.g. chimpanzees (*Pan troglodytes*, de Waal & van Roosmalen 1979), long-tailed macaques (*Macaca fascicularis*, Aureli 1992), olive baboons (*Papio anubis*, Castles and Whiten 1998) and brown capuchins (*Cebus paella*, Verbeek & de Waal 1997)], although it has been shown to occur in other mammal species [domestic goats (*Capra hircus*, Schino 1998), bottlenose dolphins (*Tursiops truncatus*, Samuels & Flaherty 2000), spotted hyenas (*Crocuta crocuta*, Hofer & East 2000), domestic dogs (*Canis familiaris*, Cools et al. 2008), wolves (*Canis lupus*, Cordoni & Palagi 2008), horses (*Equus caballus*, Cozzi et al. 2010)] and birds [ravens (*Corvus corax*, Fraser & Bugnyar, 2011)] as well.

Reconciliation reduces the likelihood of further aggression, but can also be costly because the conflict may flare up again at an attempt to reconcile. Thus, not all conflicts are reconciled and there are individual differences among dyads (Aureli et al. 2002). Factors that may influence reconciliation are cause, intensity and outcome of the conflict, kinship and relationship quality (Arnold et al. 2010). Individuals with a high quality relationship experience more post-conflict anxiety after a fight, which in turn motivates them to reconcile (Aureli 1997).

Cords & Aureli (2000) predicted relationship quality to consist of the three components compatibility, security and value. Compatibility describes the degree of affiliation and tolerance between social partners, as well as the shared history of social exchanges. Security means that behaviours are predictable and consistent over time, while value encompasses all the benefits gained by a relation, e.g. food sharing and agonistic support. The results of Fraser et al. (2008), who investigated this topic in chimpanzees (*Pan troglodytes*), confirmed the hypothesis of Cords & Aureli (2000). Similar components of relationship quality have been

found in Japanese macaques (*Macaca fuscata yakui*), though relationships were highly asymmetric (Majolo et al. 2010), ravens (*Corvus corax*, Fraser & Bugnyar 2010) and Barbary macaques (*Macaca sylvanus*, McFarland & Majolo 2011). In spider monkeys (*Ateles geoffroyi*), only two components of relationship quality were found. The first may represent both compatibility and value, while the second was labeled risk rather than security, because it contained both aggression and embraces, which can reduce the risk of aggression (Rebecchini et al. 2011).

The most prominent hypothesis concerning reconciliation is the “valuable relationship” hypothesis (Aureli et al. 1989), which states that individuals sharing a valuable relationship should reconcile more often than others, to repair the relationship and thereby preserve its benefits. Secure relationships, on the other hand, may not need to be reconciled as they may not have been damaged by aggressive conflict in the first place. It is assumed that if interactions between partners are highly predictable, the relationship should be resilient (“secure relationship” hypothesis, Schaffner & Caine 2000). The costs of reconciliation (renewed conflict) may be influenced by compatibility. For compatible partners that frequently share friendly interactions in a variety of contexts, approaching each other after a conflict may be less risky, making reconciliation more likely (Cords & Aureli 2000).

Another function of reconciliation, which is related to the repairing of relationships, is the reduction of stress, indicated by reduced self-directed behaviour after reconciliation (Aureli & van Schaik 1991). Conflict causes stress for both opponents because it damages their relationship, making their future interactions uncertain. Also, further escalations might ensue if the situation is not resolved. Reconciliation mitigates these effects and thus reduces stress (integrated hypothesis, Aureli 1997). The risk of renewal may affect the rest of the group as well and bystanders may reduce stress by engaging in affiliation among themselves (Judge & Mullen 2005). Also, the victim of a conflict is less likely to be attacked again after a reconciliation event (Aureli & van Schaik 1991). Silk (2000) built on these facts to propose, as an alternative to the valuable relationship hypothesis, that reconciliation serves merely to signal that the conflict is over and that the intentions of the participants towards each other are now benign, thus reducing stress caused by uncertainty. In several non-cooperative breeding primate species, kin have been shown to reconcile more often than non-kin (York & Rowell 1988, Aureli et al. 1989, Judge 1991, Aureli 1997). That kinship, though it provides a secure relationship, does not appear to reduce reconciliation (Silk et al. 1996) and is another argument used by Silk to promote her “benign intent” hypothesis.

Callitrichids are cooperative breeders and live in family groups usually consisting of one parent pair and their offspring. Since all individuals, except the parents, are close kin, their relationships are expected to be secure, as well as valuable because group members widely depend on each other (Schaffner & Caine 2000). However the ways in which the value and security of a relationship may influence the occurrence of reconciliation are exactly the opposite. Valuable relationships should be reconciled, secure ones not. So, even though reconciliation could help to maintain group cohesion and cooperation in cooperatively breeding groups, the high security of relationships may override any need for relationship repair and inhibit reconciliation. The results of the studies conducted so far on three Callitrichid species are contrary. Schaffner et al. (2004) did not find reconciliation in small groups of red bellied tamarins (*Saguinus labiatus*) and thus hypothesized that secure relationships need not be reconciled because conflict does not damage them. However, Westlund et al. (2000) found that reconciliation occurred in common marmosets (*Callithrix jacchus*), so cooperative breeding does not seem to be the reason for the absence of reconciliation in tamarins. Furthermore, Peñate et al. (2009) did find reconciliation in cotton-top tamarins (*Saguinus oedipus*), providing additional evidence against the “secure relationship” hypothesis.

On one hand, reconciliation in common marmoset family groups could be expected, because in several other primate species, kin have been shown to reconcile more often than non-kin (e.g. Kutsukake & Castles 2000, Castles et al. 1996). On the other hand, relationships among kin, especially if they are cooperative breeders, are expected to be secure, and secure relationships should not be damaged by conflict. Still, reconciliation is said to be driven by relationship value. Cooperative breeders may have secure relationships, but they should also be highly valuable, because cooperation is vital for the whole group, perhaps more than in other social systems. Fraser et al. (2008) found that all aspects of relationship quality were elevated among kin in chimpanzees. If secure relationships are not unique for cooperative breeders, why should security decrease reconciliation in this, but not in other, social systems?

The aim of this study was first to assess whether the three component structure of social relationships is present in common marmosets (*Callithrix jacchus*). Second, I investigated the link between differences in relationship quality and variation in reconciliation. If a component representing value acts as a predictor of reconciliation, this would imply that the valuable relationships hypothesis can also be applied to the cooperative breeding social system. If

secure relationships are reconciled less, or if there is no reconciliation and relationships are generally secure, then the secure relationships hypothesis would be supported.

Reconciliation and relationship quality in common marmosets might depend on group size and composition. Subordinate females are reproductively suppressed by the dominant female, but control over the subordinates' reproduction may be incomplete (Yamamoto et al. 2009). When a subordinate female breeds, there is competition for resources, mostly helpers, which is disadvantageous for both females and especially costly for the subordinate (Digby 1995). Furthermore, adult non-breeding males give more help in infant care than non-breeding females, so overall it may be better for dominant females to limit the number of other adult females in their group (Yamamoto et al. 2009). Indeed, Koenig (1995) reports that reproductive success is higher in groups containing many adult males. Consequently, there might be more tension and less security in larger groups with many adult female offspring, which may eventually lead to dispersal, while in small groups, the need for reconciliation might be obliterated by the security of the group members' relationships, as predicted by Schaffner & Caine (2000).

Schaffner and Caine (2000) argue that reproductive inhibition of subordinate females is a factor that precludes reconciliation in cooperative breeders. The groups studied by Westlund et al. (2000), who found reconciliation in common marmosets, consisted mainly of males and they mention that their results were possibly due to that, because reproductive inhibition could not play such an important role in their groups. In larger groups containing many adult females, there is a higher potential for conflicts and relationships might be less secure. According to Digby & Saltzman (2009), it is more likely in common marmosets than in other callitrichids that two breeding females are present in one group, leading to competition between them and even infanticide. This potential for competition between the dominant female and her adult daughters might have an effect on reconciliation. Of the three groups I observed for this study, two contained more than one adult female. For the reasons mentioned above, I expected more conflicts to occur in the group containing more females than males. In the wild, such a group might disperse when there is too much tension, but in the laboratory dispersion of a group cannot happen so easily.

If conciliatory tendencies do not vary depending on relationship quality, meaning that valuable partners do not reconcile more often, stress reduction might be the main reason for opponents to reconcile. In this case, severe conflicts, which produce more stress, should be

reconciled more often than mild conflicts. This argument that stress reduction is the main purpose of reconciliation would only be valid, though, if increased rates of self-directed behaviour after conflicts could be detected. Westlund et al. (2000) mentioned that marmosets showed no signs of being upset after conflicts, with rates of self-directed behaviour not deviating from baseline after aggressive conflict. If rates of self-scratching and self-grooming do not increase after conflicts, and decrease after reconciliation, then stress reduction may not be a motivation to reconcile.

Furthermore, the context in which a conflict occurs might influence reconciliation, as some contexts might cause more damage to the relationship than others. One context of conflict I examined is competition about access to food. In many primate species, reconciliation has been found to be reduced e.g. in brown capuchins (*Cebus apella*, Verbeek & de Waal 1997) or lacking completely like in moor macaques (*Macaca maurus*, Matsumara 1996) after food conflicts. The explanation for this is that contest competition does not damage relationships. However, this may not be true to the same extent for all species. Some primates, e.g. long-tailed macaques (*Macaca fascicularis*, Aureli 1992) do reconcile food conflicts, although less frequently than in other contexts. In contrast to other species, such as brown capuchins (*Cebus paella*) that regularly compete about food sources aggressively (Janson 1988), marmosets are usually tolerant towards each other while feeding and may even share food (Schaffner & Caine 2000). If food-related aggression is not a trivial occurrence for marmosets, relationships may suffer under such conflicts and need to be repaired. Conflict characteristics such as intensity and directionality may influence how much stress is caused by a conflict and how risky reconciliation might be.

While the minimal cognitive requirements for reconciliation are individual recognition and individualised social relationships (Aureli et al. 2002), the second kind of post-conflict behaviour I investigated in marmosets, namely consolation, is cognitively more advanced. Consolation is a post-conflict contact, not between former opponents, but between the victim and an uninvolved third party (de Waal & van Roosmalen 1979). True consolation is initiated by the third party and requires not only empathy, but also sympathy, the active response to another's distress, which may reflect the cognitive capacities of a species (de Waal & Aureli, 1996). Consolation shares the stress-alleviating function of reconciliation, but friendly post-conflict interactions between the recipient of aggression and a bystander can have other functions as well (reviewed by Fraser et al. 2009). Bystanders may reduce the risk of becoming the target of redirected aggression through affiliative contact with the victim (Call

et al. 2002). Affiliative contact may also be initiated by the opponent's kin and serve as an alternative to reconciliation if the risk of a renewed conflict between former opponents is too high (Wittig & Boesch 2003). That consolation may substitute reconciliation is also mentioned by Palagi et al. (2006), who report that consolation rates were higher in the absence of reconciliation. Additionally, they mention that the likelihood of further attacks among group-members was reduced after consolation occurred.

While a bystander offering consolation to a recipient of aggression incurs the risk of becoming a target of redirected aggression, there is no such risk if the affiliative contact was initiated by the victim (solicited consolation). Bystanders may even avoid the victim for some time after the conflict if it does not solicit consolation (Verbeek & de Waal 1997). In contrast, Schino & Marini (2012) discovered that in Mandrills (*Mandrillus sphinx*) bystanders that frequently became the target of redirection offered more affiliation to victims. Thus, bystanders may reduce the risk of redirection by initiating consolation.

This study also investigated whether consolation occurs in common marmosets. However, neither true consolation nor solicited consolation was expected (see the results of Westlund et al. 2000). It is possible that either the cognitive requirements for consolation are not present in marmosets or, as they show little sign of distress after conflicts (Westlund et al. 2000), consolation is not needed. Even if redirected aggression from the victim to bystanders occurs, it could also be that consolation might not take place. Social constraints caused by a strict hierarchy, for instance in macaques, seem to make consolation very risky, because the third party might become another target of the aggressor (de Waal & Aureli 1996). However, this could not explain an absence of consolation in marmosets due to their rather loose hierarchy.

3. Methods

3.1. Subjects and housing

Data were collected from December 1 2011 to April 14 2012 at the University of Vienna. Research subjects were three family groups (Tab. 1) of common marmosets (*Callithrix jacchus*), consisting of six, seven, and eight individuals, respectively.

Table 1. Names, sex, age and relatedness of all individuals in the three family groups observed

group	name	sex	date of birth	relatedness
Pooh	Pooh	m	14.08.1999	father
Pooh	Augustina	f	1999	mother
Pooh	Fimo	m	Aug. 2002	offspring/twin of Zaphod
Pooh	Yara	m	March 2003	offspring/twin of Pandu
Pooh	Pandu	f	March 2002	offspring/twin of Yara
Pooh	Lokri	m	Aug. 2003	offspring/twin of Messina
Pooh	Messina	f	Aug. 2003	offspring/twin of Lokri
Kiri	Kiri	f	2000	mother
Kiri	Zaphod	m	Aug. 2002	father/twin of Fimo
Kiri	Veli	f	14.11.2004	offspring
Kiri	Mink	m	15.05.2005	offspring/twin of Nemo
Kiri	Nemo	f	15.05.2005	offspring/twin of Mink
Kiri	Oli	f	15.10.2005	offspring
Kiri	Jack	m	23.03.2006	offspring/twin of Sparrow
Kiri	Sparrow	f	23.03.2006	offspring/twin of Jack
Wichtel	Wichtel	f	30.10.2005	mother
Wichtel	Kobold	m	11.04.2005	father
Wichtel	Clever	m	04.11.2009	offspring/twin of Smart
Wichtel	Smart	m	04.11.2009	offspring/twin of Clever
Wichtel	Fix	m	15.06.2010	offspring/twin of Foxi
Wichtel	Foxi	m	15.06.2010	offspring/twin of Fix

The groups were housed in adjacent indoor cages which measured 2.5m x 2.5m x 2.5m for Kiri and Pooh group and 1.25m x 2.5m x 2.5m for the Wichtel group. Each cage was connected to an additional outside cage of the same size. Since data collection started in winter and ended in spring (just before the outside temperatures were warm enough for

marmosets), the monkeys did not have access to the outdoor cages during the whole time. All cages were equipped with branches, wooden boards, baskets, ropes and various textiles. The monkeys were fed once a day with fruits, vegetables, dairy products, eggs, mealworms, etc. Feeding time was between 12:00 and 14:00, depending on the lab schedule. The temperature was kept at 26°-30° during the day and at 21°-23° at night, humidity at 40-70%. In winter, a 12h:12h dark-light cycle was maintained.

3.2. Data collection

3.2.1. Relationship quality data collection

To assess relationship quality (RQ), I conducted 10-minute focal samples and continuously recorded all social interactions between the focal animal and other group members during that time. I made observations at different times of the day, between 9:00 am and 4:30 pm. They were balanced across the week so that each monkey had the same amount of observation sessions at a given time of the day. I recorded the duration and frequency of different behaviours (see Tab. 2). Durations were recorded for allogrooming, contact-sitting, being in proximity (within one body length), anal inspection, mouth inspection and play. Additionally, I recorded which individual started the interaction and which ended it. Frequencies were recorded for threat, displacement, approach-retreat, yield, avoid and submissive vocalizations accompanied by a fear grin (“fear”). Data on passive food sharing was collected ad libitum.

Table 2. Definitions of the most important behavioural variables recorded during relationship quality and post-conflict observations and their social contexts

context	behaviour	definition
<u>affiliation</u>	proximity	actor and reactor are sitting or resting within one body length (minus the tail) of each other
	contact sit	the actor is sitting or resting in physical contact with another individual
	allogrooming	the actor parts the hair of the reactor with its hand, sometimes removing particles with its teeth
	anogenital inspect	the actor orientates face towards anogenital region of the reactor, who has its tail raised

play-related

play	the actor approaches the reactor and starts play with an initiative element, most commonly tail pull, mock bite or overrun. Other play elements follow, almost always including play wrestling. Play chase often marks the end of a play bout. A play bout is considered to have ended when at least one of the play partners turns away and focuses attention somewhere else for three seconds
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food-related

co-feeding	sitting within one body-length while both animals are eating from the food bowl
proximity at feeding site	proximity between animals sitting on the food platform while at least one of them is currently not eating
steal food	the actor successfully takes a piece of food from the reactor, who is resisting
food sharing (passive)	the actor removes a piece of food from the reactor's hand or mouth, who tolerates it
attempt to take food	the actor tries to take food from the reactor but is not successful

agonism

gecker	aggressive vocalization, series of loud, harsh elements, low frequency
threat	a gecker which did not provoke any kind of response from the recipient
submissive squeal	loud, long submissive call, high pitch and frequency
scream	more intense than submissive squeal
chase	the actor pursues a fleeing opponent
fear grin	the lips are drawn back, the teeth visible
fear	the actor is oriented towards another individual, showing fear grin and issuing long, loud submissive squeals intermitted by high whistles
yield	the actor jumps or runs away from an approaching individual
avoid	the actor leans aside or shifts body position in response to the approach of another individual
displace	the actor takes the place of the reactor after a threat
withdrawal	the actors' body is withdrawn, the arms remain extended; submissive

cringe	body withdrawn with hind legs bent and spine curved; extreme form of withdrawal
<u>self-directed behaviours</u>	
self grooming	the actor uses hands and teeth to part and manipulate fur of any reachable body region
self scratching	the actor scratches itself with toenails or fingernails

3.2.2. Post-conflict data collection

A conflict was defined as an interaction where at least one participant showed aggressive behaviour (aggressor) towards the other. The recipient of the aggression (victim) either responded aggressively or displayed submissive behaviour. To investigate the occurrence of reconciliation and consolation, I used the “PC/MC method” described by de Waal and Yoshira (1983). Whenever a conflict was observed, I conducted a 3-minute focal observation on the victim, called the “PC” (post-conflict focal). Aggression could be purely vocal (“gecker”) or include a bodily attack (scratching, hitting, biting, jumping on the other) and sometimes a chase. Submission consisted mainly of a vocalization called “submissive squeal”, sometimes accompanied by cringe or withdrawal of the body and fear-grin. Another vocalization, “scream”, was more intense than a submissive squeal and considered to indicate more severe aggression. In most cases the victim was the recipient of the aggression, only sometimes the roles of aggressor and victim reversed during the conflict, i.e. the initiator of the aggression was in the end the victim. At other times it was not possible to distinguish who attacked first or who won the conflict because neither participant showed any sign of submission or moved away. Therefore, the victim was defined as the individual that first left the site of the conflict, even if both opponents stayed in proximity after aggression had ended.

When a conflict started, I recorded the identities of both opponents, their roles (aggressor and victim, as described above), which aggressive and submissive behaviours were displayed and what caused the conflict, if obvious. Depending on the cause, conflicts were sorted into four contexts, namely “food”, “play”, “copulation” and “non-food, unclear cause”. In the first three, it was obvious from what kind of situation the conflict arose, i.e. food, play and copulation. The rest was summarized under the label “non-food”, because there was clearly no food was involved. This context may include conflicts caused by many different situations

which were, however, not distinguishable for the observer. When the conflict ended I recorded the outcome. A clear outcome means that there was a clear victim, i.e. one of the opponents submitted to the other. If the outcome was unclear, aggression ceased without one of the opponents having displayed any kind of submissive behaviour. The PC started immediately after a conflict had ended and all affiliative behaviours in which the victim was involved were recorded, as well as any aggressive and submissive vocalizations issued by or directed at the victim. Affiliative behaviours were proximity, contact sit, grooming and play. Since individuals must come into proximity before they can move into a contact sit or start grooming, proximity was the first affiliative behaviour recorded, with the exception of play. When play is about to start, it is obvious from the characteristic expression (“play face”) and other initiative elements, even before the partners come into proximity (Volland 1977). Proximity as a conciliatory behaviour can be effective in reducing post-conflict anxiety even when it does not result in grooming (McFarland & Majolo 2013). Aggressive and submissive interactions during the PC must be completely one-sided, hence only vocal, for the PC to continue. Reciprocated aggression or an aggressive response to submissive behaviour during the PC means that the conflict was renewed. Consequently, the PC was terminated, the new conflict recorded and a new PC started. For renewed conflicts, only the last, uninterrupted PC was used. If the victim attacked another individual during the PC, this was called “redirected” and again the original PC was terminated, the new conflict recorded and the PC conducted with the new victim as focal individual. Likewise, if the victim was attacked again during the PC, but by a different aggressor, the same procedure was used. All conflicts involving the same victim, but different aggressors, were called “previous conflicts” of this victim.

Additionally, self-directed behaviours were recorded as indicators of stress (Barros et al. 2004). The marmosets displayed only two kinds of self-directed behaviours, namely self-scratching and self-grooming (Bassett et al. 2003). Body-shaking and yawning were not observed. Other stress-indicating behaviours described for common marmosets, namely scent marking and increased locomotion (Bassett et al. 2003) were not taken into account.

Table 3. Descriptions of conflict characteristics and contexts of conflicts and the types that were recorded for each of them

variable	type	description
body contact	yes/no	conflict with bodily attack by at least one of the opponents
context	non-food	no food was involved and the cause of the conflict was not obvious
	food	conflict over access to food
	play	conflict resulting from a play situation which got out of control
	copulation	one or more individuals attack the copulating pair
chase	yes/no	the victim is chased by the aggressor during the conflict
directionality	unidirectional	only one of the opponents shows aggressive behaviour of any kind
	bidirectional	both opponents show aggressive behaviour
outcome	clear	there is a clear winner of the conflict, the loser shows submissive behaviour or retreats
	unclear	there is no clear winner when the conflict stops; aggression ceases but none of the opponents submits or retreats
previous conflicts	number of	number of conflicts with other opponents the victim was involved in prior to the current conflict; the PC focals of all previous conflicts were interrupted by a new conflict
redirected	yes/no	the aggressor of the current conflict was originally the victim of an earlier conflict, but attacked another monkey during the PC focal
renewed	number of	conflict between the same opponents flares up again during the PC focal
reversed	yes/no	roles of aggressor and victim reverse within a conflict, so that the original aggressor becomes the victim
renewed-reversed	yes/no	renewed conflict with reversed roles
victim scream	yes/no	used as indicator of the severity of the attack; scream is more intense than submissive squeal

When a conflict occurred, it inevitably interrupted an ongoing RQ focal because I did not divide the observation time in post-conflict and relationship quality recordings. Instead, I conducted RQ focal samples in which conflicts were recorded ad libitum. If the RQ focal individual was involved in a conflict as the victim, I continued the RQ focal and used the three minutes following the conflict as a PC focal. If a conflict occurred and the RQ focal individual was not the victim, I interrupted the RQ focal for three minutes to conduct a PC focal on the victim of the conflict. After the end of the PC period, I continued the RQ on the original focal animal.

The second part of the PC/MC method is the matched control focal (MC). It was conducted within one week at the same time of the day of a recorded conflict and PC. Again, the former victim was observed and the same behaviours recorded as during the PC. This matched control focal (MC) controlled for baseline affiliation between the victim and the aggressor or the victim and other group members. During MC observations the same behaviours as during PCs were recorded and during both it was noted which individual initiated any observed interaction. The MC only started if the focal individual was not involved in any conflict for at least two minutes prior to the MC starting time. Like PCs, MCs were not taken into account if interrupted by conflicts. In contrast to other studies using this method, I allowed former opponents to be in proximity when the MC started. In marmosets, the opponents often remain in proximity (Westlund et al. 2000) after a conflict and I wanted to control for this. MCs were either taken from a 10-minute RQ focal, or, if the former victim was not scheduled for a RQ focal at the correct time of the day, conducted between RQ observations. When a MC did not fit into the schedule within a week of the PC, the PC was discarded. Accordingly, 209 PC/MC pairs could be used for post-conflict analysis, although I recorded a total of 277 conflicts. Nonetheless, all 277 conflicts served as ad libitum data for the relationship quality analysis.

All sessions were video recorded and coded using the program Solomon Coder and Microsoft Excel 07. SPSS versions 19 and 20 were used for statistical analysis.

3.3. Data analysis

3.3.1. Relationship quality analysis

Relationship quality variables recorded during the 10-minute focal samples were entered into a principal component analysis (PCA) following the statistical methodology of Fraser et al. (2008) to find out the composite measures of marmoset relationship quality. In this analysis all behaviours recorded in the RQ focals were used, as well as the ad libitum data on passive food sharing and conflicts. Additionally, grooming symmetry was calculated for each dyad using the formula $[A \text{ grooms } B / (A \text{ grooms } B + B \text{ grooms } A)] + 1$, with A being the individual who groomed less. For some dyads, no grooming was recorded. Other dyads displayed completely one-sided grooming. To differentiate between these two options, “+1” was added to the formula, so that “no grooming” resulted in scores of 0 and “one-sided grooming” in scores of 1. All other grooming symmetry scores ranged between 1 and 1.5, which represented completely symmetrical grooming. Components with a minimum eigenvalue of 1 after extraction were considered principal components and high loadings were considered to be above 0.5 or below -0.5. Variables with communalities lower than 0.45 were excluded from the analysis. Variables that loaded alone on a component (e.g. displacement) were also taken out. Variables that remained in the PCA were contact sit, proximity, grooming, tolerance around food, play, conflicts, yield, avoid and fear (PCA1). All further analyses including RQ components were done with the variables generated by this PCA. A second PCA (PCA 2) containing the additional variable “variability of affiliation” was added later on. Variability of affiliation was calculated with the coefficient of variation ($CV = \sigma / \mu$) of contact sit and grooming. A high CV means that there were many fluctuations in these behaviours between months. The contact sit and grooming durations for each month and each dyad were summed up and divided by the number of focal samples available for that month.

The possible influences of relatedness (parent-parent, parent-offspring, offspring-offspring) and sex combination on relationship quality components were tested using generalized linear mixed models (GLMMs). Identities of the dyad and group were added as random variables to account for the non-independence of data points stemming from the same individual and the same group. Akaike’s Information Criterion (AIC) was applied to select the best, most parsimonious model and only significant independent factors represented in the best model.

To find out if the components of relationship quality differed among the three groups, Kruskal-Wallis tests were applied. Mann-Whitney U-tests were conducted as post hoc tests. Because multiple comparisons were made among the three groups, Bonferroni corrections were used and the new α -level was 0.017.

3.3.2. Post-conflict analysis

MC/PC pairs were rated as “attracted” (A), “neutral” (N) or “dispersed” (D), depending on the timing of affiliative interactions between former opponents during PC compared to MC. If opponents came together earlier in the PC than in the MC, the conflict was labeled “A”; if at the same time or not at all during either PC or MC, the conflict was labeled “N”, and if they met earlier in the MC than in the PC, it was labeled “D”. The individual proportions of “A” versus “D” pairs were calculated for all individuals who were the victims of at least three conflicts. They were tested for normal distribution using a Kolmogorov-Smirnov test ($p=0.886$ for the proportion of attracted and $p=0.439$ for the proportion of dispersed PC/MC pairs) and compared in a paired T-test to find out whether reconciliation took place at all. A survival analysis was then calculated to find out if the temporal distribution of interactions differed between PC and MC. Furthermore, the “Corrected Conciliatory Tendency” (CCT, Veenema et al. 1994) was calculated, again for all individuals with at least three conflicts, using the formula $(A-D)/(A+D+N)$. To obtain information on how sex and rank (meaning in this case parent versus offspring) might influence individual CCTs, a linear mixed model (LMM) was calculated. CCT was the dependent variable; fixed variables were sex, rank and the interaction of sex and rank. Group identity was entered as a random variable.

The amounts of friendly interactions initiated by the former victim and by the former aggressor were compared between PC and MC focals in a Chi-square test.

To assess consolation, PC/MC pairs were again rated as attracted, neutral or dispersed, depending on whether the victim came into proximity with a bystander sooner during the PC or during the MC. Proportions of attracted and dispersed PC/MC pairs were calculated, checked for normal distribution (Kolmogorov-Smirnov test, $p=0.945$ for the proportion of attracted and $p=0.999$ for the proportion of dispersed PC/MC pairs) and compared in a paired T-test. The test was repeated with $n=11$ after eliminating the victims which showed “fear” and “yield” for their former opponent after the conflict, assuming that it was unlikely they would interact with bystanders while focusing their attention on the former aggressor. Two more

victims exhibited “fear” and “yield” behaviours towards bystanders and the test again repeated after eliminating them from the analysis (remaining $n=9$), as interactions with bystanders also seemed unlikely while the victim was afraid of them. To compare the timing of interactions during PC and MC, a survival analysis was computed.

Self-directed behaviours (SDBs) have been used in many studies as reliable behavioural indicators of stress (e.g. Majolo et al 2010). Self-scratching and self-grooming were lumped for analysis. For each individual with at least three conflicts, SDB rates (bouts per minute) during PCs and MCs were divided by the total number of PC/MC pairs. As the mean SDB rates were normally distributed (Kolmogorov-Smirnov test, $p=0.973$ for PC and $p=0.928$ for MC SDBs), a paired T-test was used.

3.3.3. Reconciliation analysis

Reconciliation might be influenced by several factors, such as characteristics of conflicts (see Tab. 3), PC submissive vocalizations and aggressive vocalizations (threats), sex combination and relatedness of dyads and relationship quality. Relationship quality variables used in this analysis were the three components the PCA had yielded. To find out which variables had a significant effect, a binomial generalized linear mixed model (GLMM) was conducted. The dependent variable reconciliation was created by transforming how each conflict was rated (A, D or N) into a binomial variable with $A=1$ and $D, N=0$. In other words, a conflict was either deemed reconciled when former opponents met earlier during the PC than during the MC (1), or not reconciled when former opponents met earlier during the MC or not at all during either PC or MC (0). Group and identities of aggressor and victim were entered as random variables. The best model was selected via AIC model selection and included the independent variables outcome, category, renewal, directionality, submissive vocalizations and value. Multiple comparisons were made for conflict category and renewal. For both, the Bonferroni-corrected α -level of 0.00416 was applied.

To find out which of the variables that make up the component value was responsible for its effect on reconciliation, a Mann-Whitney U-test was calculated for each variable, with reconciled/not reconciled as the group variable.

4. Results

4.1. Relationship quality

4.1.1. Components of relationship quality

One aim of my study was to find out which aspects of relationship quality might influence reconciliation. To test this, components of relationship quality were extracted from the data via principal component analysis. The PCA 1 yielded three components, explaining 67.41 % of the total variance (Tab. 4). Principal components were those with a minimal eigenvalue of 1 and high loadings were scores ≤ -0.5 and ≥ 0.5 . The first component explained 30.745% of variance and contained high loadings for conflict and submissive to fearful behaviours, thus representing the opposite of secure relationships as described by Cords & Aureli (2000). Thus, it was labeled “insecurity”. Grooming symmetry had the highest negative loading on this component. Contact sit, grooming, grooming symmetry and proximity loaded highly on the second component, which was called “value”, because grooming and symmetrical grooming can be considered beneficial for an individual. The second component explained 21.234% of the variance. The third component had high loadings for tolerance around food and play, as well as proximity, whereas conflict loaded negatively on it. Since feeding situations often result in conflict, social partners who often feed together but have little conflicts seem to be tolerant to each other and frequently interact non-aggressively. I therefore considered the third component to represent “compatibility” and it explained 15.431% of the variance.

Table 4. Varimax rotated matrix of the three principal components. Components were extracted with an eigenvalue of at least 1 and high loadings (bold) were scores ≤ -0.5 and ≥ 0.5 . The three principal components explained 67.41% of the total variance

	component		
	1	2	3
conflicts	.676	-.061	-.474
yield	.926	-.175	-.030
fear	.839	-.059	-.032
avoid	.939	-.080	-.033
contact sit	-.083	.783	-.023
grooming	-.027	.851	.041
grooming symmetry	-.398	.544	-.073
proximity	-.036	.647	.529
play	-.061	-.103	.688
tolerance around food	-.046	.127	.745
% of variance explained	30.745	21.234	15.431

The PCA 1 did not include any information about the consistency of relationships over time, which, according to the literature, should be another composite measure of security.

Therefore, the variability of affiliation was calculated and included in the PCA 2 later on (Tab. 5). It was expected to have high loadings on the insecurity component.

The PCA 2 explained 63.917% of the total variance. The loadings of all previously present variables actually did not change compared to the PCA 1, but variability of affiliation did not load highly on insecurity. Instead, it had a high negative loading on value. In the PCA 2, insecurity explained 28.033% of variance, value explained 21.547% and 14.337% were explained by compatibility.

Table 5. Varimax rotated component matrix including the variable variability of affiliation. Components were extracted with an eigenvalue of at least 1 and high loadings (bold) were scores ≤ -0.5 and ≥ 0.5 . The three principal components explained 63.917% of the total variance

	component		
	1	2	3
conflicts	.681	-.087	-.457
yield	.918	-.179	-.041
fear	.836	-.080	-.028
avoid	.937	-.127	-.022
contact sit	-.052	.798	.012
grooming	.005	.843	.090
grooming symmetry	-.376	.510	-.020
proximity	-.017	.557	.590
play	-.074	-.134	.678
tolerance around food	-.052	.110	.741
variability of affiliation	.224	-.601	.013
% of variance explained	28.033	21.547	14.337

4.1.2. Factors influencing relationship quality

For each of the relationship quality components obtained in the PCA, a GLMM was calculated with sex and relatedness as fixed variables. Neither sex combination nor relatedness had a significant effect on insecurity (Fig. 1), although post hoc tests revealed a tendency for offspring-offspring dyads to be more insecure than parent-offspring dyads ($B=0.458$, $SE=0.256$, $t=1.791$, $p=0.078$).

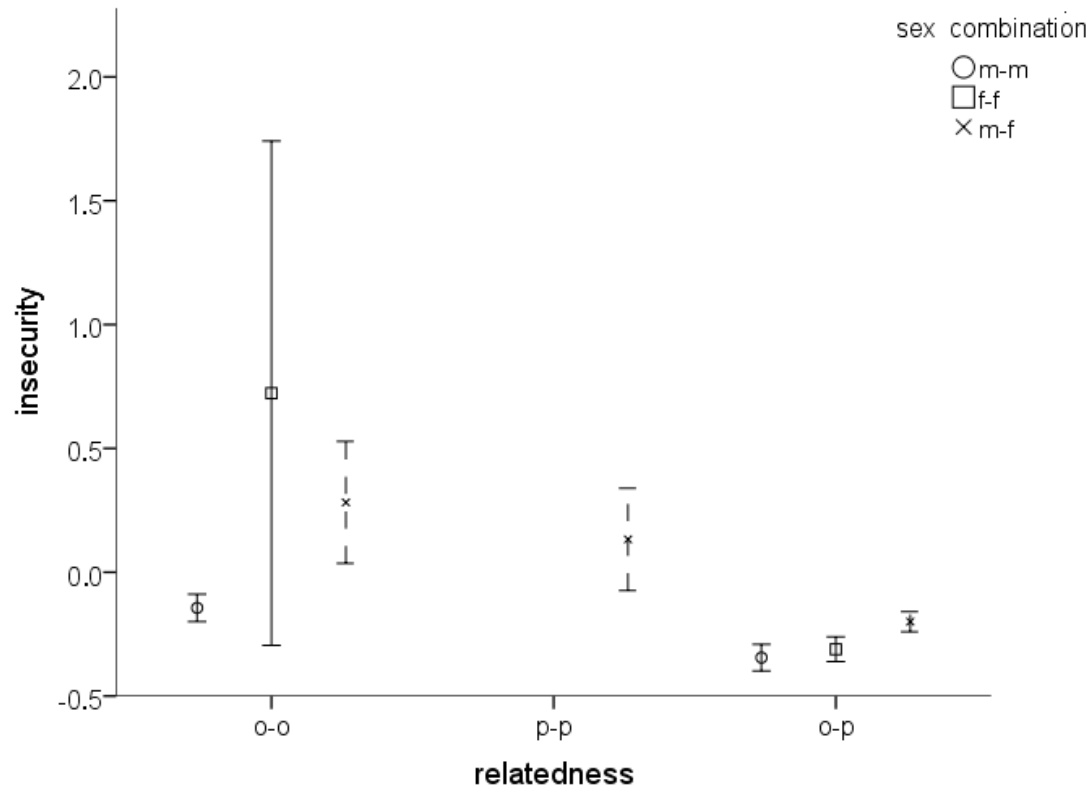


Figure 1. Mean scores ($\pm$ SE) of insecurity (component 1) for relatedness (o=offspring, p=parent) and sex combination (m=male, f=female)

Only relatedness had a significant influence on value ($F=19.2$, $df=2$, $p\leq 0.001$, Fig. 2). Relationships of offspring-offspring dyads ($B=0.510$, $SE=0.2$, $t=2.554$, $p=0.013$) and parent-parent dyads ($B=2.639$, $SE=0.445$, $t=5.929$, $p\leq 0.001$) were more valuable compared to parent-offspring dyads. Parent-parent dyads were also more valuable compared to offspring-offspring dyads ($B=2.128$, $SE=0.464$, $t=4.59$, $p\leq 0.001$).

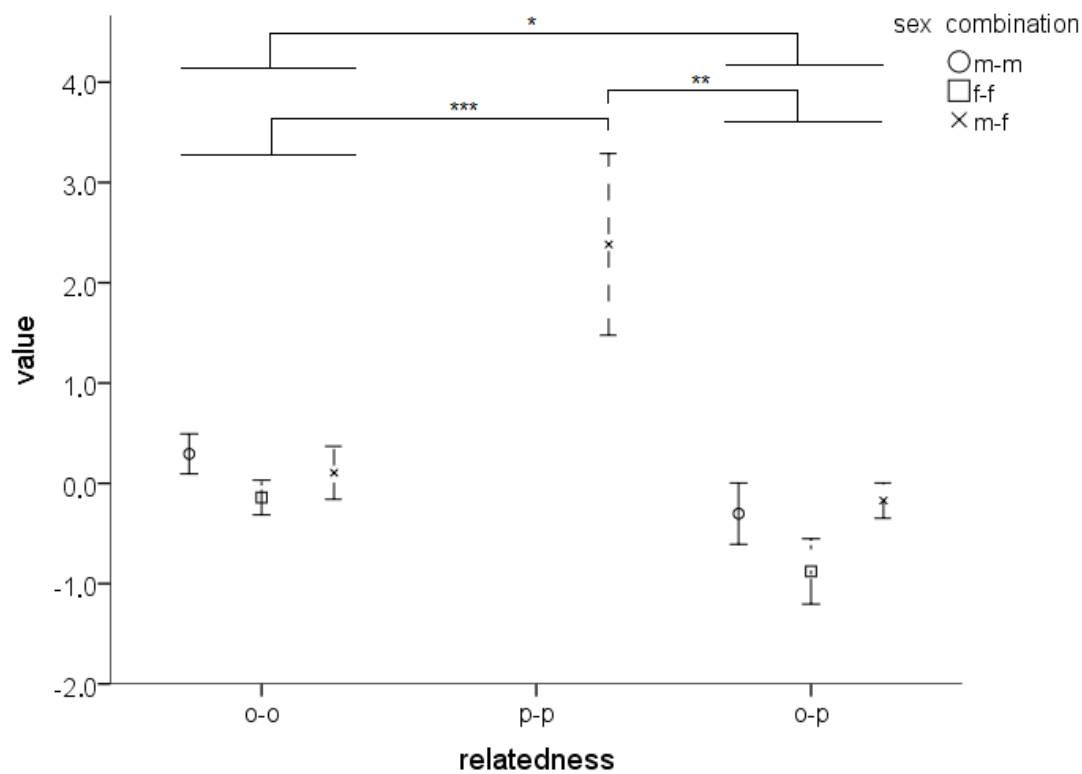


Figure 2. Mean scores ($\pm SE$) of value (component 2) for relatedness (o=offspring, p=parent) and sex combination (m=male, f=female)

Compatibility was affected by both sex combination ($F=6.307$, $df=2$, $p=0.003$) and relatedness ($F=4.838$, $df=2$, $p=0.011$, Fig. 3). More compatible relationships were found among male-male dyads ($B=0.721$, $SE=0.258$, $t=2.791$, $p=0.007$) compared to male-female dyads, and offspring-offspring dyads ($B=0.776$, $SE=0.23$, $t=3.374$, $p=0.001$) compared to parent-offspring dyads.

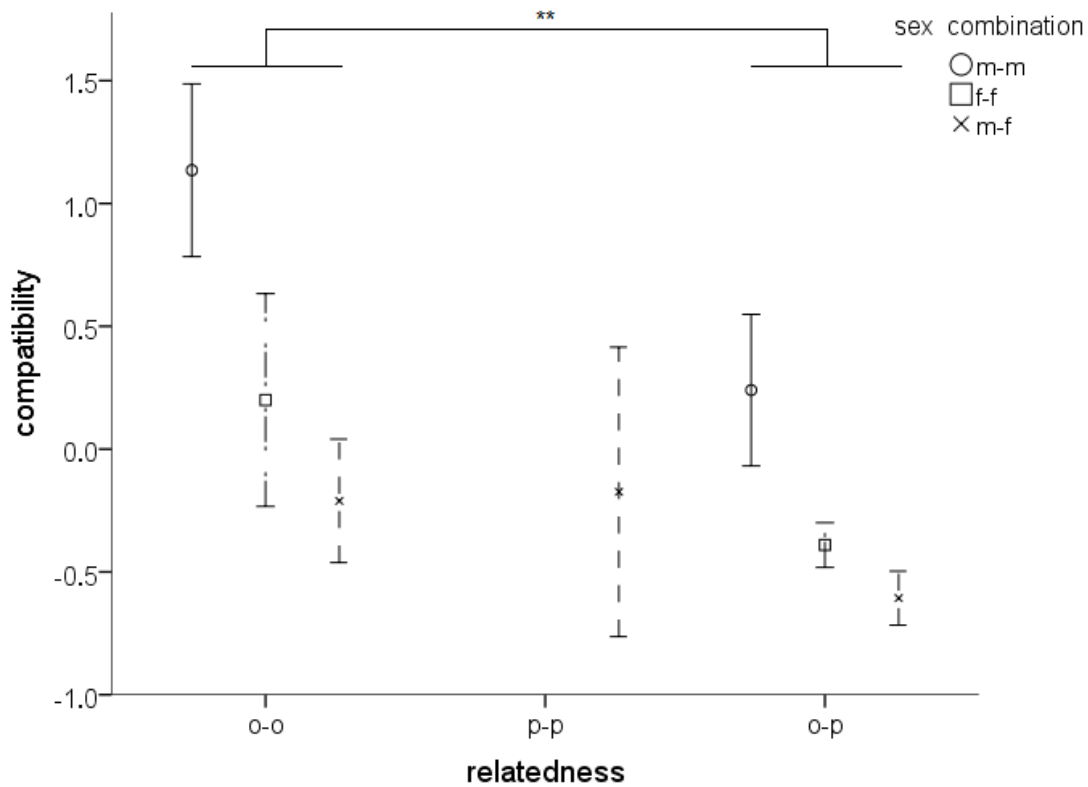


Figure 3. Mean scores ($\pm SE$) of compatibility (component 3) for relatedness (o=offspring, p=parent) and sex combination (m=male, f=female)

4.1.3. Group differences in relationship quality

Group differences in relationship quality were tested with a Kruskal-Wallis test for each component. There were differences between groups in value ($\chi^2=12.149$, $df=2$, $p=0.002$, Fig. 4) and post-hoc tests (Mann-Whitney U-tests) revealed that relationships in the Pooh group were more valuable than in the Kiri group ($Z= -3.637$, $p\leq 0.001$).

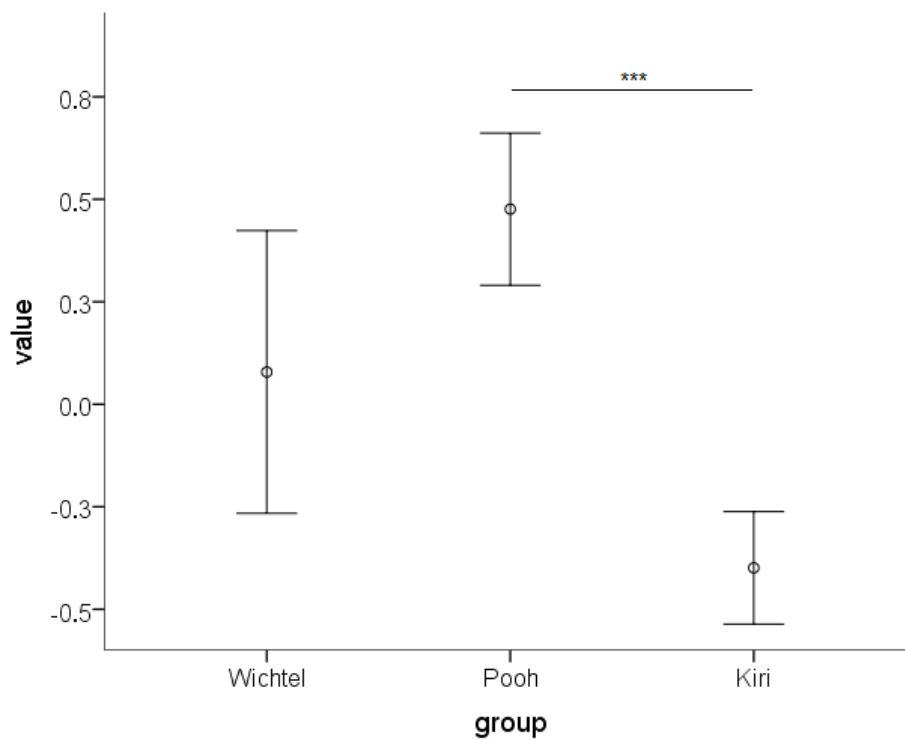


Figure 4. Mean scores ($\pm$ SE) of value (component 2) for the three family groups

Groups also differed in their mean score for compatibility ($\chi^2=13.337$, $df=2$, $p=0.001$, Fig. 5), because relationships in the Wichtel group were more compatible than in the Kiri group (Mann-Whitney U-test, $Z= -3.669$, $p\leq 0.001$) and the Pooh group ($Z= -1.973$, $p=0.049$, n.s. due to Bonferroni correction).

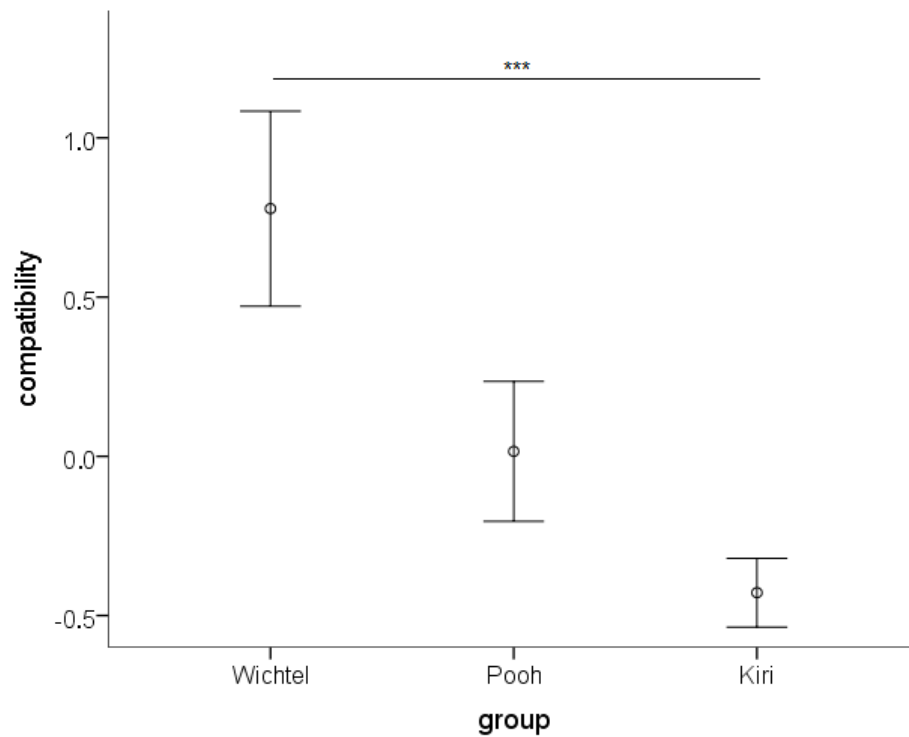


Figure 5. Mean scores ($\pm$ SE) of compatibility (component 3) for the three family groups

No group differences could be found for insecurity (Fig. 6). Some relationships in Kiri groups were extremely insecure, hence the large standard error, but the overall difference between this and the other groups was not significant.

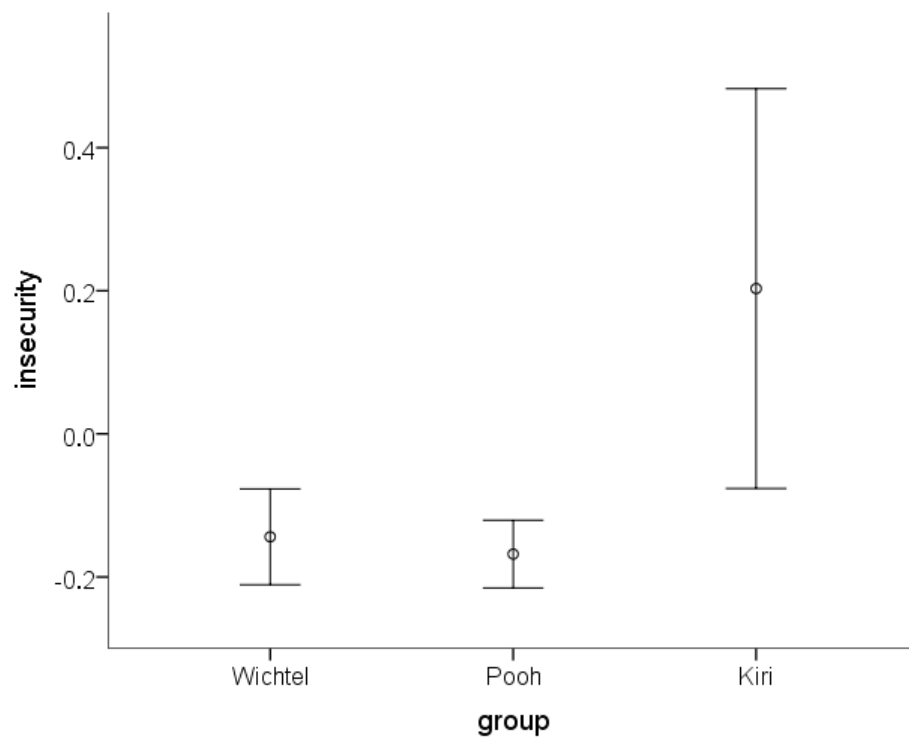


Figure 6. Mean scores ($\pm$ SE) of insecurity (component 1) for the three family groups

4.2. Post-conflict behaviours

4.2.1. Reconciliation

To find out whether marmosets reconciled conflicts or not, the mean proportions of attracted and dispersed PC/MC pairs for all individuals with at least three conflicts were compared. The subjects showed significantly more affiliative behaviour towards a former opponent after a conflict than in control periods (paired T-test, $T = 3.192$, $df = 13$, $N = 14$, $p = 0.007$, Fig. 7).

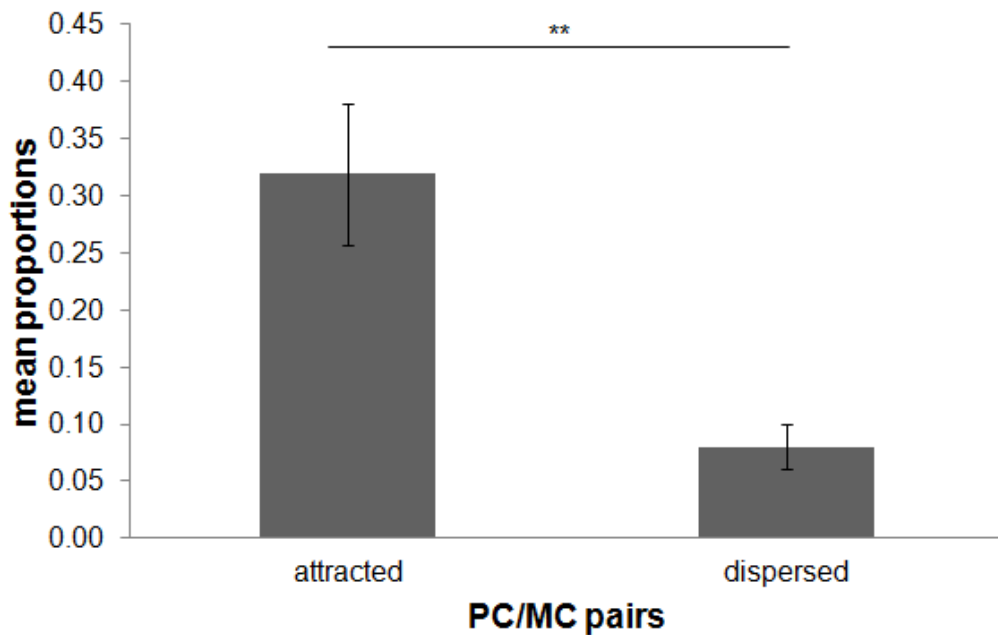


Figure 7. Mean proportion of attracted (affiliation during PC earlier than during MC) and dispersed (affiliation during MC earlier than during PC) PC/MC pairs

Former opponents did not only meet more often after conflicts, but they also met earlier than during control periods. This was demonstrated by the survival analysis that compared the timing of affiliative interactions in PC and MC focals ($\chi^2 = 23.586$, $df = 1$, $p \leq 0.001$). Most instances of affiliation during the PC happened within one minute after the end of aggression, while there was no such pattern during MC periods (Fig. 8). Former opponents remained in proximity in 12.44% of all conflicts, in 20.1% they separated first and came together later. In the remaining 67.45%, former opponents did not come together after the conflict. On average, former opponents came together after 28.43 seconds, excluding the cases where there was no

post-conflict reunion. The comparison of mean SDB (self-directed behaviour) rates for PCs and MCs yielded no significant result.

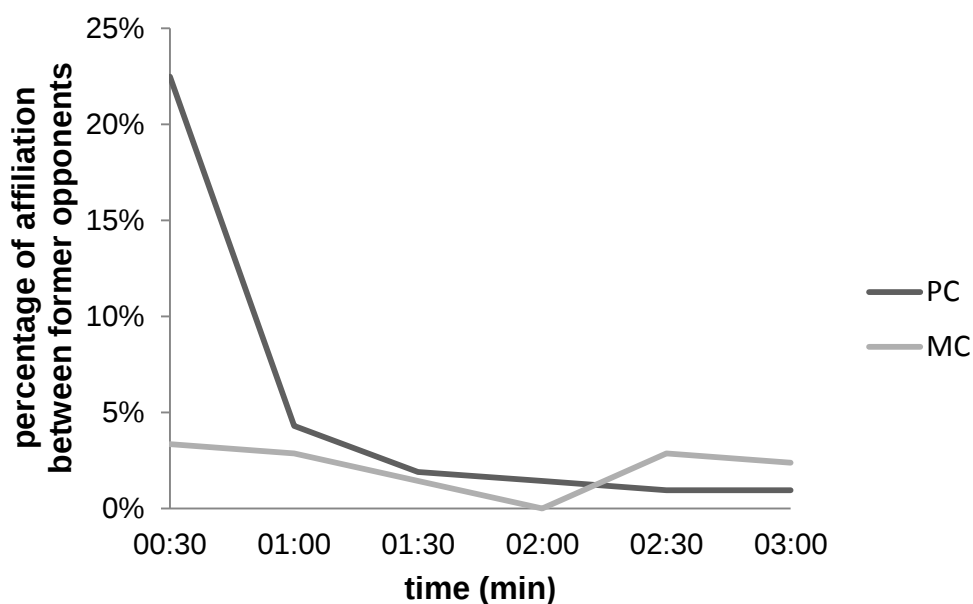


Figure 8. Distribution of affiliative interactions between former opponents over the 3 minutes following the end of a conflict (PC) compared to the control period (MC)

Individual corrected conciliatory tendencies averaged at 28.07%, but varied a lot (SD=29.91%). The LMM testing for effects of sex and rank on individual CCTs showed that sex alone had no influence ($F=1.677$, $df=1$, $p=0.224$). However, rank ($F=13.638$, $df=1$, $p=0.004$) and the interaction of sex and rank ($df=1$, $F=5.0921$, $p=0.048$) did have a significant influence on CCTs. Post-hoc tests showed that the CCTs of offspring were lower than the CCTs of parents ($B= -0.66$, $SE=0.165$, $t=-3.991$, $p=0.003$) and that female offspring had higher CCTs than all others ($B=0.501$, $SE=0.222$, $t=2.257$, $p=0.048$).

Friendly interactions after a conflict was more often initiated by the former victim than by the former aggressor, compared to the control period ($\chi^2=5.852$, $df=1$, $p=0.016$)

4.2.2. Consolation

The comparison of the proportions of attracted versus dispersed PC/MC pairs for victims coming into proximity with a bystander showed that there was a trend for victims to do so more often after a conflict ($T=1.872$, $df=12$, $p=0.086$).

There was also a trend for affiliation between victims and bystanders to occur earlier in PC than in MC periods, as the survival analysis of third-party interactions showed ($\chi^2=0.12$, $df=1$, $p=0.073$). This means that though the timing of third party interactions was similar during PC and MC focals (Fig. 9), victims tend to interact with bystanders slightly earlier during the PC. Interaction rates among the marmosets were generally high. It was very likely at any given time that the focal individual would soon come together with another group member. During both PC and MC, the latency of the of the victim interacting with any of the other group members excluding the former aggressor were very short, hence both curves peak at the beginning and then level out.

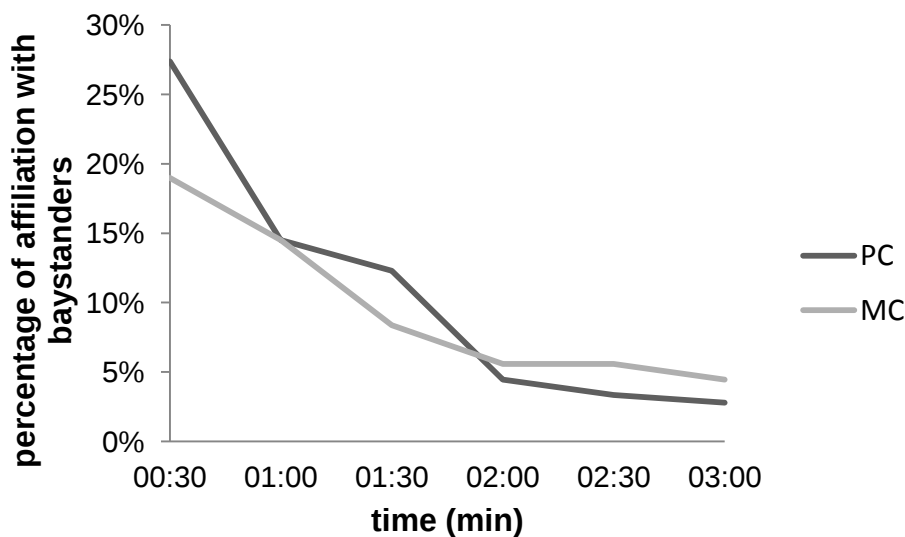


Figure 9. Distribution of affiliative interactions between the victim of a conflict and a third party over the 3 minutes following the end of a conflict (PC) compared to the control period (MC)

Furthermore, the PC interactions with bystanders were initiated by the victims more often than the MC victim-bystander interactions ($\chi^2=5.122$, $df=1$, $p=0.024$).

4.2.3. Factors influencing reconciliation

To find out which factors influence reconciliation, I ran a GLMM on a number of variables which might contribute to or inhibit reconciliation, including conflict characteristics, vocalizations during the PC and relationship quality. Variables that remained in the best model were directionality ($F=5.696$, $df=1$, $p=0.018$, Fig. 10), outcome ($F=12.713$, $df=1$, $p\leq 0.001$, Fig. 11), submissive vocalizations by the victim during PC ($F=9.338$, $df=1$, $p\leq 0.001$, Fig. 12), relationship value of the opponents ($F=8.660$, $df=1$, $p=0.004$, Fig. 13), renewed conflict ($F=4.480$, $df=3$, $p=0.005$, Fig. 14) and conflict category ($F=7.964$, $df=3$, $p\leq 0.001$, Fig. 15). The time span from 0 to 180 seconds after conflict was used to visualize the results of conflict characteristics significant in the GLMM.

Unidirectional conflicts were reconciled more often than bidirectional conflicts ($\beta = -1.255$, $SE=0.526$, $t = -2.387$, $p=0.018$, Fig. 10). The number of bidirectional and unidirectional conflicts was almost equal, with 49.8% bidirectional conflicts.

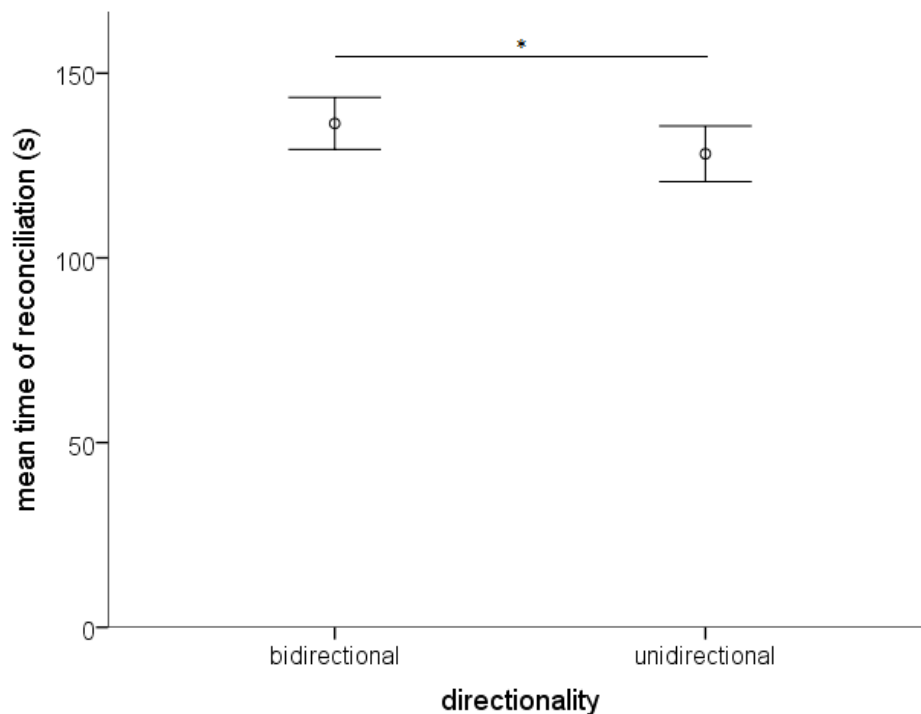


Figure 10. Mean time of reconciliation, ($\pm SE$) for bidirectional and unidirectional conflicts

Conflicts with unclear outcome that yielded no clear winner or loser, were reconciled more often than those with a clear outcome ($\beta = -2.102$, $SE = 0.589$, $t = -3.565$, $p \leq 0.001$, Fig. 11).

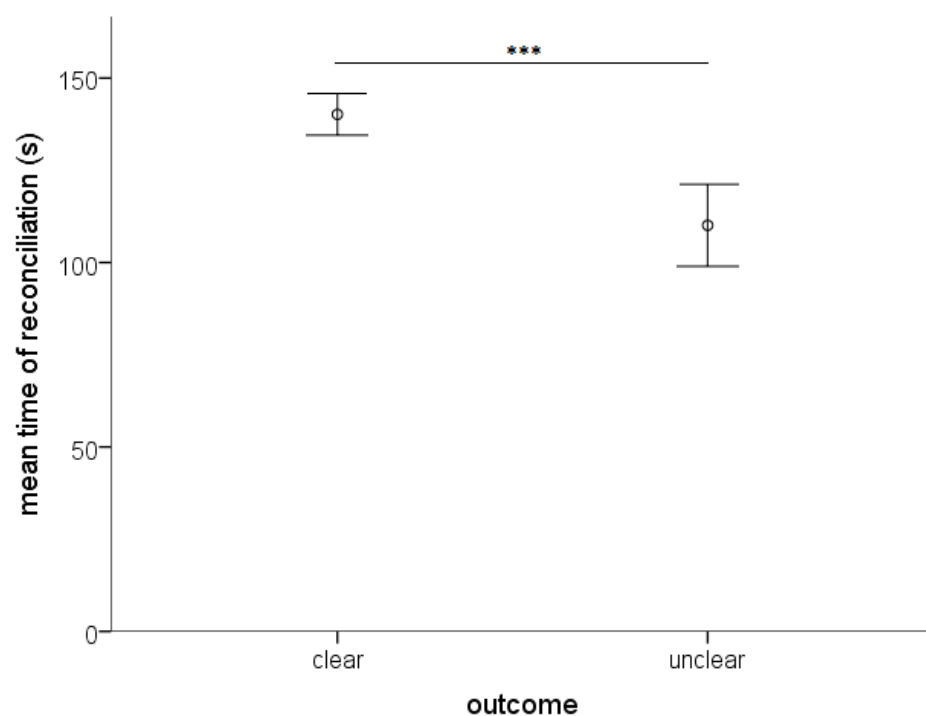


Figure 11. Mean time of reconciliation ($\pm SE$) for conflicts with clear and unclear outcome

There was more reconciliation when submissive vocalizations were given by the victim during the PC compared to when there were no submissive vocalizations ($\beta=2.837$, $SE=0.927$, $t=3.059$, $p=0.003$, Fig. 12). Note that per definition, vocalizations that were made when moving into proximity with the former opponent were included.

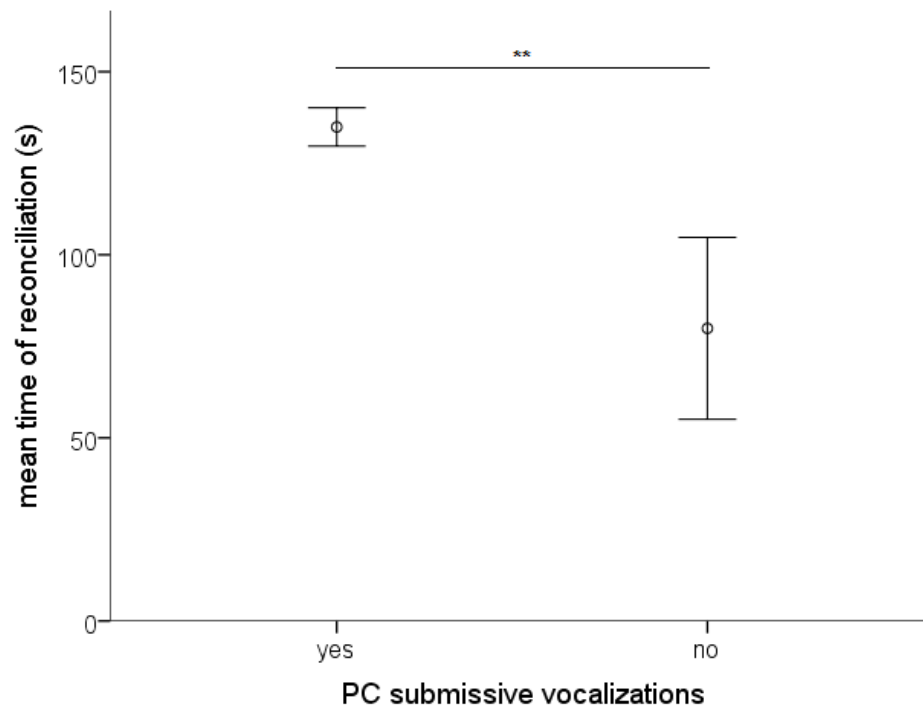


Figure 12. Mean time of reconciliation ($\pm SE$) when submissive vocalizations either did or did not occur during the PC

Valuable partners were more likely to reconcile their conflicts ($\beta = -0.642$, $SE = 0.218$, $t = -2.943$, $p = 0.004$, Fig. 13). The Mann-Whitney U-tests showed that the amount of grooming within the dyad influenced the likelihood of reconciliation ($Z = -2.66$, $p = 0.008$), as did grooming symmetry ($Z = -3.073$, $p = 0.002$). Contact sit had a significant influence as well ($Z = -2.288$, $p = 0.022$), which is not surprising considering that marmosets are automatically in contact when they groom each other. When only contact sit without grooming (e.g. monkeys resting or sleeping in contact) was taken into account, the significance disappeared. Proximity had no significant influence on reconciliation.

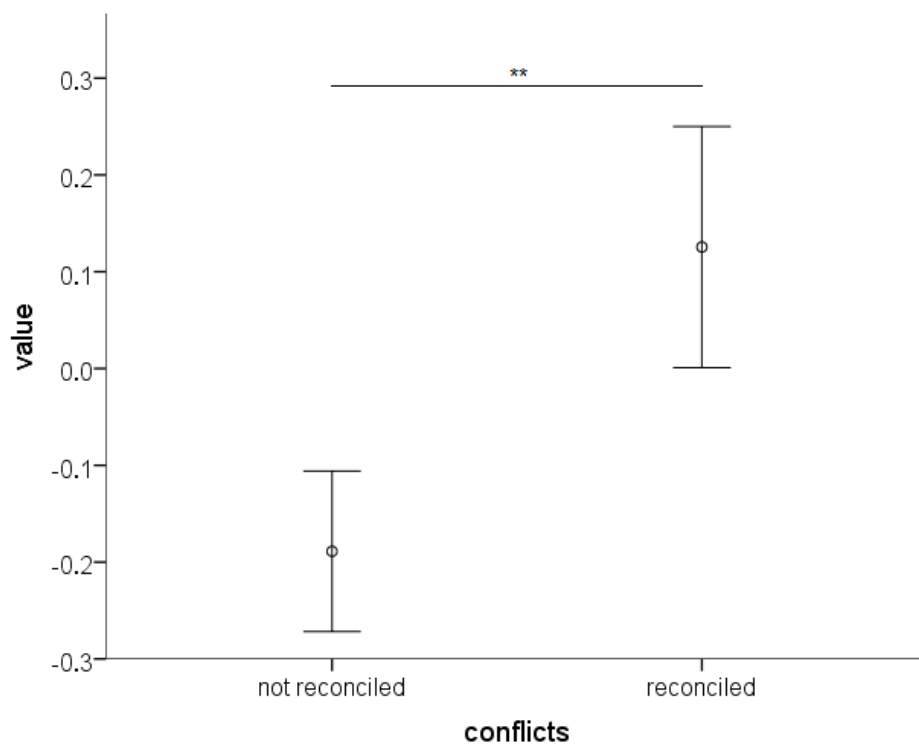


Figure 13. Mean relationship value ($\pm SE$) of opponents for not reconciled and reconciled conflicts

Conflicts that were renewed at least three times were reconciled more often than conflicts renewed only once ($\beta=4.799$, $SE=1.311$, $t=3.662$, $p\leq 0.001$), or not at all ($\beta=3.207$, $SE=1.102$, $t=2.910$, $p=0.004$). All other combinations were not significant (Fig. 14). Renewal occurred in 27.7% of food conflicts and in 11.2% of non-food conflicts and only in one case was a renewed non-food conflict reconciled.

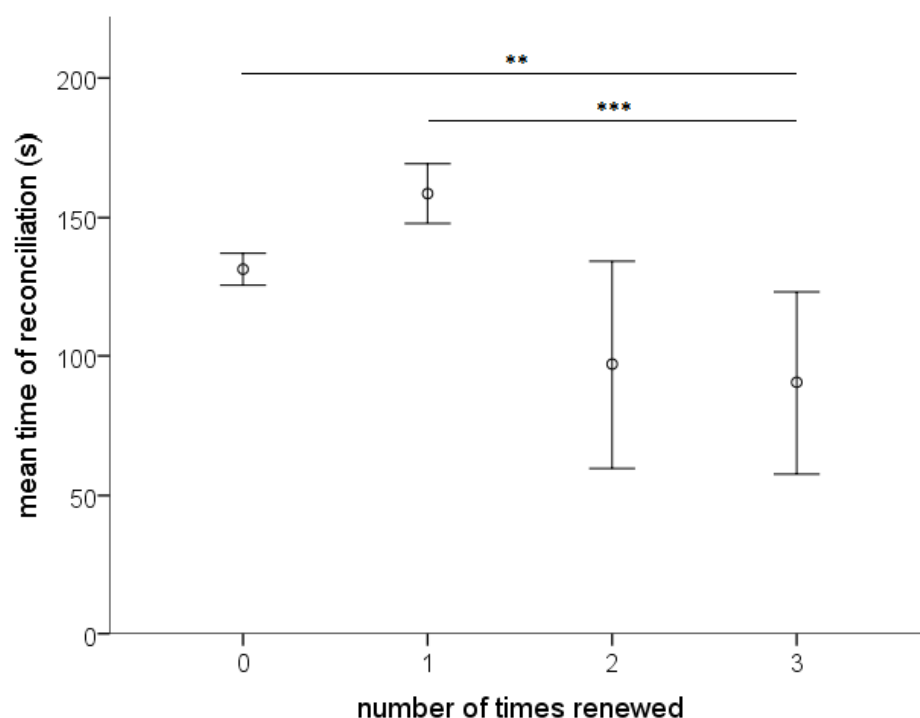


Figure 14. Mean time of reconciliation ($\pm SE$) when a conflict was not renewed (0), renewed once (1), twice (2) or at least three times (3)

Reconciliation also depended on the context of a conflict. Reconciliation was less likely after conflicts of the category “non-food conflict of unclear cause” ($\beta=2.791$, $SE=0.778$, $t=3.587$, $p\leq 0.001$) compared to copulation conflicts. Play conflicts were reconciled more often than non-food conflicts ($\beta=2.928$, $SE=1.012$, $t=2.894$, $p=0.004$) and there was also more reconciliation after food conflicts than after non-food conflicts ($\beta=1.923$, $SE=0.47$, $t=4.092$, $p\leq 0.001$). In short, non-food conflicts of unclear cause were reconciled less often than conflicts of all other categories. There were no significant differences between copulation, food and play conflicts (Fig. 15).

After food conflicts, former opponents met at the food bowls after food conflicts in 34% of all cases and elsewhere in the cage only in 3.2%. Play conflicts were followed by play in 50% of all cases and never by any other activity. Copulation conflicts occurred only in the Kiri group. Whenever the parent pair was copulating, one or both adult sons attacked them until they managed to separate the parents. Then the conflict was over and the situation immediately relaxed, with some or all participants staying together or moving into proximity within 10 s of the conflict in 77.8% of all cases and a contact later ensued in 33.3%. After non-food conflicts, in contrast, opponents came into proximity in only 18% of all cases, i.e. in 11.2% they did not separate and in 6.7% they came back together later on. Contact sit occurred in only 3.4%.

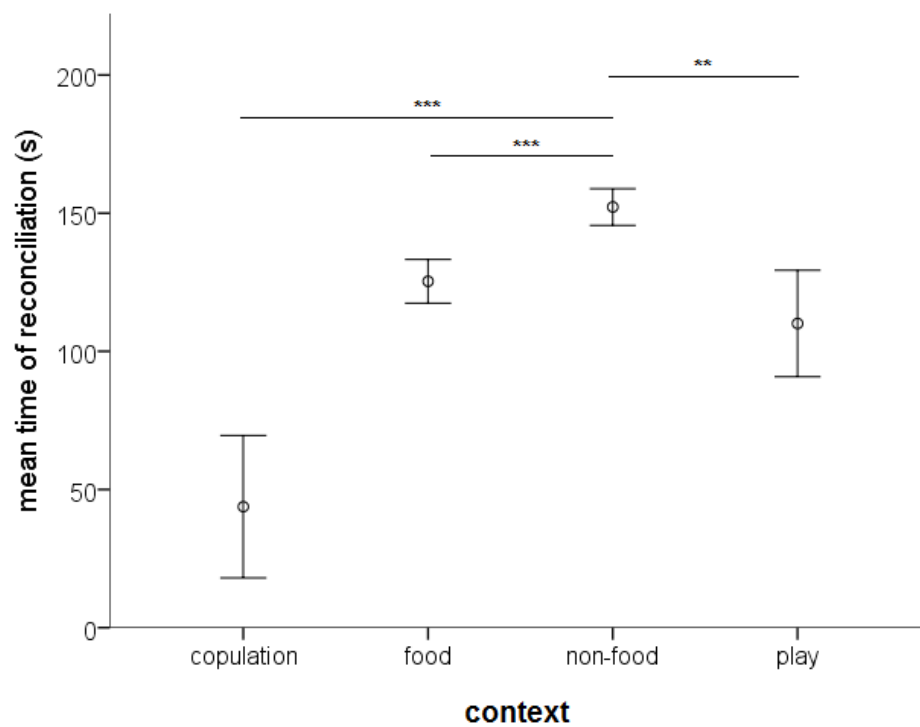


Figure 15. Mean time of reconciliation ($\pm$ SE) for the four different conflict categories

Variables not represented in the best model were redirection, previous conflicts, reversal, body contact, victim scream, chase and threats during the PC. Relatedness and sex combination of conflict partners were also not significant in the GLMM and thus, not present in the best model. However, a Kruskal-Wallis test on the time of reconciliation (from 0 to 180 seconds) yielded significant results for relatedness ($\chi^2=8.604$, $df=2$, $p=0.014$) and sex combination ($\chi^2=8.372$, $df=2$, $p=0.015$, Fig. 16). Further analyses (Mann-Whitney U-tests) showed that there was more reconciliation among parent pairs than offspring dyads ($Z= -2.884$, $p=0.004$) and that male-male dyads reconciled more often than female-female dyads ($Z= -2.426$, $p=0.015$) and male-female dyads ($Z= -2.837$, $p=0.005$). There was no difference in reconciliation between the three family groups.

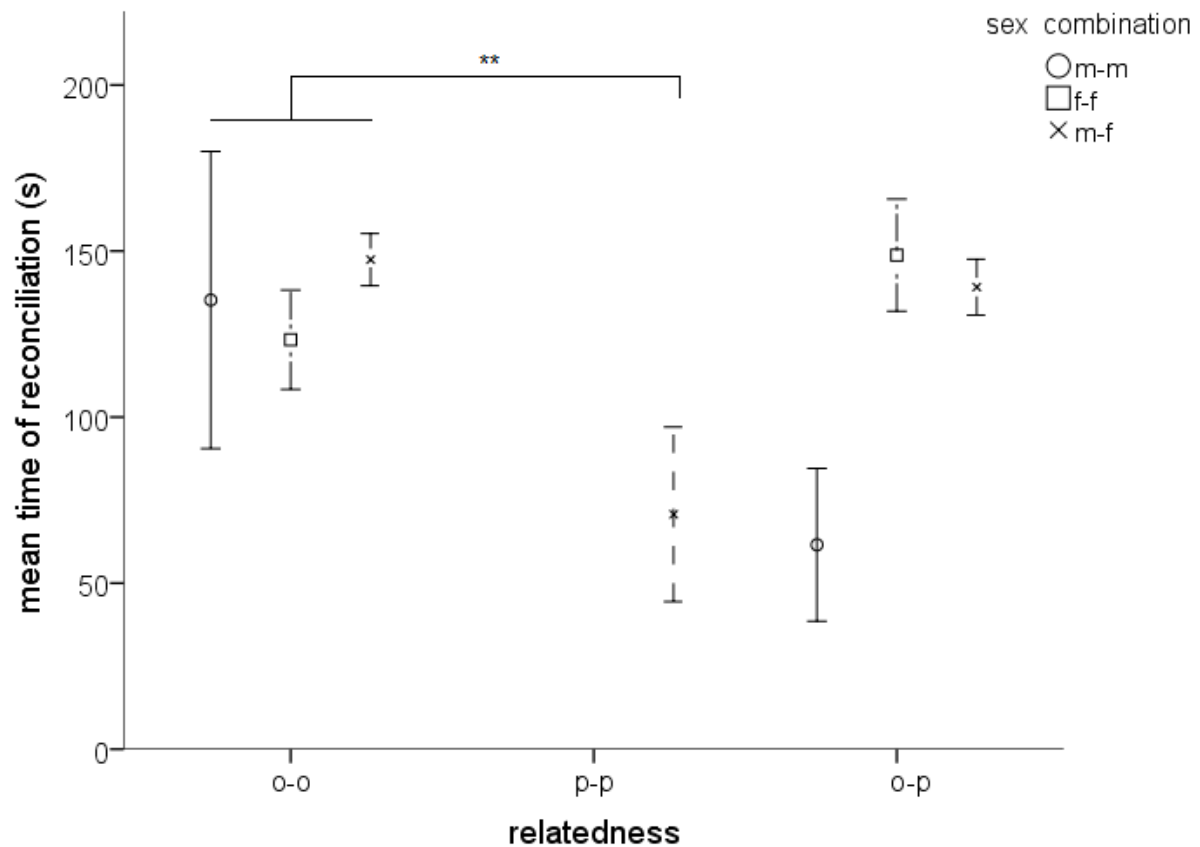


Figure 16. Mean time of reconciliation ($\pm$ SE) of dyads with different relatedness (o=offspring, p=parent) and sex combination (m=male, f=female)

5. Discussion

5.1. Relationship quality

Marmoset relationship quality consisted of the three principal components: value, compatibility and (in)security, a structure which was first predicted by Cords & Aureli (2000) and since then found in several primate species with different social systems [chimpanzees (*Pan troglodytes*, Fraser et al. 2008), Japanese macaques (*Macaca fuscata yakui*, Majolo et al. 2010) and Barbary macaques (*Macaca sylvanus*, McFarland & Majolo 2011)]. In the only other New World monkey species investigated so far, spider monkeys (*Ateles geoffroyi*), only two components were found (Rebecchini et al. 2012). Each species has its own specific behaviours and even similar behaviours may part of different components. This makes comparisons difficult, but supplies information on how relationships are organized in each species. The component explaining most of the variance in marmoset relationships was insecurity. Insecure relationships in marmosets are often interrupted by conflict and marked by evasive behaviours, which show that one of the dyad is not comfortable with being close to the other. Cords & Aureli (2000) described secure relationships as consistent over time, but this pattern did not emerge in the current study. Variability of affiliation is the opposite of consistency and was therefore expected to load on insecurity. Instead, it was part of value. Value, the second component, also comprised the behaviours proximity, contact sit, grooming and grooming symmetry. The fact that grooming and grooming symmetry were present in the same component coincides with the observation of Lazaro-Perea et al. (2004) that marmosets prefer to groom those individuals from which they in turn received grooming. Perhaps marmosets further prefer to groom those social partners who are consistent in their affiliation, which would explain the negative loading of variability of affiliation on this component. Value, in the sense of Cords & Aureli (2000), encompasses all benefits gained from a relationship. The marmosets, though, did not engage in behaviours which marked value in other species, such as agonistic support, active food sharing or successful begging (begging attempts were only made by the offspring in the Wichtel group, only towards their mother and were never seen to be successful). However, there is at least some evidence that grooming represents a direct benefit in marmosets, and thus value. Lazaro-Perea et al. (2004) observed that dominant female marmosets use grooming as a reward for helper-females. This is one reason why the second component was labeled value and the third component compatibility. Compatibility in common marmosets consisted of proximity (the only behaviour loading highly on two components), play and tolerance around food. The latter could also be

interpreted as a benefit obtained from a relationship and thus, as an indicator of value. Likewise, passive food sharing, or tolerated food steal, which had to be taken out of the analysis, would also have been part of the third component. Still, the third component had an almost high negative loading of conflict, which was the other reason why the second and third components were labeled like this. An absence of conflict seemed consistent with the description of compatibility as a history of tolerant and non-aggressive interaction by Cords & Aureli (2000).

In many respects, the relationship quality components of marmosets seem very similar to those of Japanese macaques described by Majolo et al. (2010). In both cases, grooming, grooming symmetry and proximity were present in the value component, proximity during feeding (here referred to as tolerance around food) was present in compatibility and the third component represented insecurity with high loadings of aggression or conflicts. The two big differences were agonistic support, which was not observed in this study, and variability of affiliation. In macaques (Majolo et al. 2010) and chimpanzees (Fraser et al. 2008), the equivalent variables were part of the component security (or insecurity in the case of Japanese macaques), which was not the case in the marmosets.

Even within the closely related marmoset family groups, there were differences depending on the relatedness and sex combination of dyads in two of the three components, namely value and compatibility. Though there were huge differences in the insecurity scores of dyads, these differences were not caused by sex combination or relatedness. The most insecure relationships were found in Kiri group, but this group also contained some very secure relationships, so that no group differences emerged. The most valuable relationships were found in the parent pairs, followed by offspring dyads. Parent-offspring dyads had the least valuable relationships. This seems to be contrary to what is known about marmosets in the wild, i.e. that parents rely on offspring for help in raising siblings and that offspring in exchange profit from the secure territory and the protection of the group (Digby 1995). This should be conducive to valuable relationships between parents and offspring. Perhaps this is true for groups where parents regularly reproduce. The groups observed for this study, however, were not reproducing any more. Not only were parent-offspring relationships the least valuable, parent-offspring dyads had furthermore less compatible relationships compared to offspring-offspring dyads. Relationships were also more compatible among males than among females, which seems adequate for a social system where there may be competition among females regarding their reproductive status (Digby & Saltzman 2009).

5.2. Reconciliation

5.2.1. Forms of reconciliation

Reconciliation consisted mainly of proximity between former opponents. Any specific behaviours or vocalizations which were characteristic of reconciliation in all contexts were not observed. Context did not only affect the frequency of reconciliation, but also determined which form reconciliation took. In the majority of all cases, former opponents came into proximity soon after a conflict and no other interactions ensued. Proximity resulting in contact sit, or even grooming, was observed mainly after copulation conflicts. Copulation conflicts occurred only in the Kiri group, where about half a year after the observations ended one of the daughters gave birth. The conflicts where one or both adult sons attacked the parent pair whenever they copulated may have been caused by those ongoing changes in the group structure. Interestingly, all agonistic behaviours ceased immediately when the parents were separated and all or some involved individuals remained together, often moved into contact soon afterwards and sometimes even started grooming. Play during the PC was specific to play conflicts. Play conflicts happened when either one partner did not want to play anymore and the other did not want to stop, or when play got too intense. After the conflict, play was continued in most cases. When this was not the case, opponents parted and did not come together again during the PC. Play typically occurred during times of activity, so it seems conclusive that former opponents did not engage in any other affiliative behaviour such as contact sit. After food conflicts, former opponents met almost exclusively at the feeding place. Other conflicts were summarized under non-food context, though they may have had many different causes. Characteristic to this context was the large number of conflicts after which the opponents did not separate. When these cases were excluded, only a very small number of reconciled conflicts remained.

5.2.2. Factors influencing reconciliation

In general, reconciliation rates may be influenced by the strictness of the dominance hierarchy (Thierry et al. 2008). Directionality, or the amount of counter aggression, reflects how strict, or despotic, the hierarchy of a primate species' social system is. A high percentage of unidirectional conflicts that covaries with kin bias of reconciliation is characteristic of more despotic social systems in macaques (Thierry 1985, Thierry et al. 2008). In macaques, CCTs are higher the more egalitarian a species' social systems is and high CCTs are associated with explicit contact after conflicts. Bergstrom & Fedigan (2013) searched for a correlation

between directionality and kin bias in a New World monkey species, white-faced capuchins (*Cebus capucinus*), but it was not apparent. Therefore, the pattern of covariation found across macaque species might not be present in New World monkeys. Kin bias can of course not be measured in family groups of marmosets, but the high percentage of bidirectional conflicts indicates that their dominance structures are not very strict. The amount of bidirectional aggression equals the second-highest score reported for macaques by Thierry et al. (2008), but the marmosets' mean CCT is closest to the fifth-highest macaque score. Despite their high degree of tolerance, marmosets have relatively low CCTs when compared to macaques. The CCTs given by Thierry et al. (2008) measure reconciliation among non-kin, though.

The context of conflict had a strong impact on the probability of reconciliation. Conflicts of the non-food context were reconciled less often compared to food, play and copulation conflicts. In other species, food conflicts are reconciled less often than non-food conflicts (Janson 1988, Verbeek & de Waal 1997). In marmosets, the opposite could be observed.

Of the many conflict characteristics, only three significantly influenced reconciliation, namely directionality, outcome, and renewal. The conflict characteristics body contact, chase and "victim scream", thought to represent the intensity of a conflict did not influence reconciliation in the marmosets. The majority of studies investigating the topic found either that low intensity-conflicts were reconciled more often or that intensity had no effect. Only a few reported that high intensity led to increased reconciliation (reviewed by Arnold et al. 2011). Bidirectional conflict may have a positive influence on reconciliation in tolerant monkey species, such as in black macaques (*Macaca nigra*, Petit & Thierry 1994a). Marmosets, though they are a tolerant species, reconciled unidirectional conflicts slightly more often. Viewed together with the result for outcome, this seems contrary. There was more reconciliation after conflicts with unclear outcome, and after unidirectional conflict, but unidirectional conflict automatically means that the outcome was clear. In unidirectional conflicts the victim responded to the aggression only with submissive vocalizations. Submissive vocalizations may serve to appease the aggressor, so victims may benefit from quick submission and thus unidirectional conflict. If, however, the victim counters with aggression, reconciliation is more likely when both opponents prove to be equal, i.e. the outcome is unclear. In other words, the victim should either submit immediately or not at all to facilitate reconciliation.

The observed influence of renewed conflicts was the opposite of what was expected. A renewed conflict is the main risk of reconciliation and if the risk is too high, former opponents should not come into proximity. The marmosets, however, reconciled more often if a conflict was renewed two or more times. Multiple renewals occurred in all contexts, but only one renewed non-food conflict was reconciled, so the result for renewal seems to be caused by food conflicts. Reconciliation was further influenced by submissive vocalizations during the PC. They might aim to appease the aggressor, while at the same time showing that the victim was aware of the risk of renewal and not entirely comfortable in the aggressor's presence. Like multiple renewals, submissive vocalizations were associated with reconciliation only in the food context. Only when food was involved did victims vocalize while approaching or being approached, but stay in proximity with the former aggressor. If a victim was persistent, the former aggressor might relent and accept its presence, which will allow the victim to feed earlier. In the non-food context, victims making submissive vocalizations towards the former aggressor also yielded, i.e. ran away, whenever the former aggressor came near, showing that they were not prepared to incur the risk of renewal in the absence of food. After play and copulation conflicts, no submissive vocalizations occurred. Finally, it could be demonstrated that the former opponents' relationship affected reconciliation because valuable partners reconciled more often. Valuable relationships increase the partners' reproductive success, therefore reconciliation, by preventing a valuable relationship from being interrupted, ultimately increases fitness (Watts 2006).

Though there was less reconciliation among offspring than between parent pairs, no influence of relatedness on reconciliation emerged when regarded in combination with other variables. This was probably caused by the difference in value between these combinations of relatedness. Parents had more valuable relationships and thus there was more reconciliation between parent pairs. Differences in reconciliation between different kinds of dyad (sex or relatedness) may reflect the fitness benefit gained from that constellation (Cooper et al. 2005). For mountain gorillas, where only male-female dyads reconciled (Watts 1995), and hamydras baboons (Colmenares & Lazaro-Perea 1994), it has been proposed that the fitness benefit may be especially high for breeding pairs. Within marmoset family groups, parent dyads may also gain the greatest fitness benefit from their relationship, thus have a more valuable relationship and reconcile more often. Increased reconciliation could also be found among male-male dyads. Though they had more compatible rather than valuable relationships, this could also

represent a fitness benefit. Males are the more active helpers and there is no reproductive competition among them as there is among females (Yamamoto et al. 2009).

Reproductive suppression among females, or its absence in mostly-male groups, did not influence reconciliation, as suspected by Westlund et al. (2000). On the contrary, negative corrected conciliatory tendencies (CCTs) were found only in the Wichtel group, where the mother was the only female. However, the effects of reproductive suppression should be investigated in groups where the parents are still reproducing rather than in groups with old, non-reproducing parents. Caro et al. (1995) reported that female marmosets stop reproducing at a maximum age of 10 and fertility is already decreased a lot at an age of 7. According to these numbers, all of Pooh group and the mother of Kiri group were already nearing reproductive termination. In the Kiri group, which contained the most female offspring, one of the daughters actually became a mother later on, so reproductive suppression and the typical dominance structure may not have been intact anymore during data collection. It is possible that the low CCTs of the all-male offspring in Wichtel group were caused by an age effect. For a New World species, spectacled leaf monkeys (*trachypithecus obscura*, Arnold & Barton 2001a) and chimpanzees (*Pan troglodytes*, Arnold & Whiten 2001) it has been reported that adult-juvenile dyads reconciled less. In Wichtel group the majority of the sons' conflicts was with their mother and there was little reconciliation between them, resulting in low CCTs.

5.2.3. Motivation behind reconciliation

The results provide little evidence for the secure relationships hypothesis in common marmosets. The absence of recognizably elevated stress levels offer some support for the prediction that the relationships of cooperative breeders should be resilient to any negative consequences of conflict. However, conflicts were reconciled and this was not influenced by a dyad's insecurity. There was no increase in reconciliation between opponents with high insecurity scores, which would be expected according to the secure relationships hypothesis. It was noticeable though that the most insecure dyad who generally avoided each other still came together occasionally after conflicts. It should be noted that any discussion about the security or insecurity of relationships is complicated by the definition of the terms. Schaffner & Caine (2000) referred to security in the sense of predictability of interactions over time, while the component insecurity used here did not contain any measure of the relationships' predictability. The variable providing this information, variability of affiliation, loaded not on

insecurity, but on value. Security here rather means an absence of conflict and evasive behaviours in a dyad.

The finding that valuable partners reconciled more often supports the valuable relationship hypothesis. This could mean that marmosets do need to repair relationships. Still, the strong tendency of former opponents continuing their pre-conflict activity when coming together, already reported by Westlund et al. (2000) and also present in this study, makes it difficult to draw any clear conclusions about relationship repair. Thus, affiliative PC-interactions between former opponents can be interpreted in two different ways: Former opponents coming together might do so to restore tolerance, which is more important for valuable partners than for those sharing a less valuable relationship. However, it could also signify that no harm was done to the relationship, enabling them to continue as usual, which valuable partners do more often because they have a general preference for each other. The difference in interaction rates during PC and MC may have been caused by the fact that when a conflict occurs, there was, in the majority of cases, a previous interaction, while at the beginning of most MCs, no previous interaction took place. Thus, there were no increased rates of former opponents coming together at the beginning of MCs. From this point of view, the results do not directly oppose the secure relationships hypothesis. An experimental approach such as Cords' (1992) could give future studies the opportunity to distinguish between these two possibilities.

Reconciliation can signal willingness to retain a valuable relationship in its current form, thus preventing a loss of benefits in the future (Watts 2006) and social bonds can enhance an individual's reproductive success (Schülke et al. 2010). Therefore relationship repair through reconciliation may ultimately provide a fitness benefit, though this hypothesis needs further confirmation from long-term studies (Watts 2006). In the short term though, there may be more immediate benefits gained by reconciliation, such as access to food. Cooper et al. (2005) proposed this as an alternative explanation because relationship quality did not influence reconciliation in male Assamese macaques (*Macaca assamensis*). Although this was not the case with the marmosets, even if only food conflicts were taken into account, it might still apply to them. As mentioned before, in other species conflicts over food are usually reconciled less, while the marmosets showed increased reconciliation in the food context. Access to the food bowls may have been the main reason for marmosets to reconcile after food conflicts, as former opponents came together exclusively at the feeding place when they had had a conflict over food. Westlund et al. (2000) not only analyzed conflicts over food

from the feeding place, but also conflicts over nuts, a food that was not clumped, was easy to monopolize and quickly consumed. If the purpose of reconciliation after food conflicts is access to food, there would be little reason to approach a former opponent after a nut conflict, as the nut would quickly be eaten by the opponent. Indeed, Westlund et al. (2000) reported that nut conflicts were rarely reconciled. So the victim would probably not approach the aggressor if it had found food somewhere else or if the food was already gone. The positive influence of value means that the marmosets attempted feeding next to their former opponent more often if the relationship was a valuable one. With a less valuable partner, they might prefer to wait or approach a food bowl occupied by a different monkey. Consequently, at least in the food context, value seems to fulfill the function attributed to compatibility by Cords & Aureli (2000). It may facilitate reconciliation without being the reason for reconciliation.

Approaching a valuable partner after a conflict when no food was involved might also bring a short-term benefit, namely to facilitate grooming after a conflict. Valuable partners spend much time grooming each other, but they rarely do so after a conflict. Conflict seems to inhibit the occurrence of grooming for some time. Lazaro-Perea et al. (2004), who observed marmosets in the wild, mentioned that grooming was not associated with agonism and that both agonistic interactions and grooming between a dyad were only in a few cases observed during the same day. Similarly, during the three minutes of the PC, most former opponents coming into proximity did not start to groom or even establish contact. If grooming is for some reason unlikely to occur after a conflict, then coming into proximity might help to shorten the grooming-free period.

Though proximity as a conciliatory behaviour can be sufficient to restore tolerance (Cords 1993), implicit reconciliation in most species consists of contact behaviours such as grooming and body contact (Arnold et al. 2011), which were very seldom observed in the marmosets. Arnold et al (2011) suggest that reconciliation may not involve body contact in species that do not engage in a large variety of friendly behaviour, such as sooty mangabeys (*Cercocebus torquatus atys*, Gust & Gordon 1993) and patas monkeys (*Erythrocebus patas*, York & Rowell 1988). Furthermore, in tolerant primate societies explicit reconciliation is more common as it may be more effective in repairing relationships (Arnold et al. 2011). Marmosets do not fit into this pattern because they have a tolerant system but only reconcile in the most implicit way, by proximity. A possible explanation could be that their living as family groups provides them with a certain degree of security, in the sense of stability of the group structure, so that they do not need specific conciliatory behaviours to repair their

relationships. If it does not take much to return the relationship to its previous state, coming into proximity may be sufficient and conflicts might not be perceived as very stressful. In some cases though, conflict did appear to be disturbing for the victim. Those individuals frequently were the target of aggression and they displayed a very high baseline level of SDBs, instead of merely an increase after aggression. Signs of distress after a conflict included constant orientation towards the aggressor while showing fear, yield and avoid behaviours. This suggests that marmoset groups are resilient to conflict to a certain degree due to their need to cooperate. As relationships are not severely threatened by conflict and/or are easily restored, temporal elevation of stress after conflicts cannot be detected. When competition becomes too intense though and conflict too frequent, the damage may not be repaired, which causes permanent elevation of stress levels and, in the wild, probably dispersal.

5.3. Consolation

The functions of consolation include stress reduction (Fraser et al. 2008) and it may substitute reconciliation (Das 2000). True consolation, defined as unsolicited affiliation by a bystander towards a victim of aggression (de Waal & van Roosmalen 1979), has only been found in great apes so far and seems to be absent in monkeys (de Waal 2008). Therefore, it was not surprising that true consolation was not present in common marmosets. There was a tendency only for victims to come into proximity with a bystander more often after a conflict, similar to the solicited bystander interactions observed in brown capuchins (*Cepus apella*, Verbeek & de Waal 1997). In contrast to the capuchins, who used behaviours also associated with courtship, affiliation between marmoset victims and bystanders rarely included contact behaviours and no specific signals. Post-conflict affiliation consisting of socio-sexual behaviours initiated by the bystander has been found in stump-tailed macaques (*Macaca arctoides*) and has been interpreted as a means for bystanders to protect themselves (Call et al. 2002). To truly console others, however, the ability to develop sympathetic concern is needed. This makes it more complex than state-matching and emotional contagion, though not as sophisticated as perspective taking, which allows targeted helping (de Waal 2012). In order to react empathically, the emotional state in oneself which was induced by another individual needs to be attributed to the other and not the self (de Waal 2008). The self-representation required for such a response can be gauged by an individual's ability to recognize itself in a mirror, as mirror self-recognition and advanced empathy appear to develop together in both ontogeny and phylogeny (de Waal 2008). In the experiments of Burkhardt & Heschl (2007),

marmosets showed basic perspective taking in the sense that they can use the knowledge of what others know. But they failed in a mirror self-recognition task that was sensitive to negative as well as positive outcomes (Heschl & Burkhardt 2006): A dab of chocolate cream was placed on the marmosets' foreheads, which they tried to lick off their reflections' faces. Despite this misapprehension, they were capable of using mirrors instrumentally. In both regards, marmosets are very similar to all other monkey species hitherto tested (Heschl & Burkhardt 2006).

6. Conclusion

Taken together, this thesis showed two main findings: i) The three-component structure of relationship quality could be confirmed for common marmosets, although a clear distinction between security, value and compatibility according to the predictive framework of Cords & Aureli (2000) was not apparent. No component fitting the theoretical description of security emerged, instead the first component was termed insecurity. The consistency of affiliation over time, thought to represent security, was part of the component termed value. This made it impossible to test the role of security (as described by Schaffner & Caine 2000, Cords & Aureli 2000, Aureli et al. 2002 etc.) in the marmosets' post-conflict behaviour.

ii) The current study found that common marmosets reconciled conflicts, albeit mainly through continuing their previous activity. Factors influencing reconciliation were the outcome, directionality and context of a conflict, as well as the relationship value of former opponents and the occurrence of submissive vocalizations by the victim. While this could be seen as support for the valuable relationships hypothesis in cooperative breeders, considerable doubt remains concerning the function of reconciliation. An experimental approach might be better suited to investigate the question whether relationships were harmed by conflicts and repaired through reconciliation, or never damaged at all, allowing former opponents to continue their previous activity after the interruption.

7. References

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8. Appendix

8.1. Abstract

Reconciliation, the post-conflict reunion between former opponents, varies among different primate social systems, because social structures influence relationship quality, especially value. Value encompasses all benefits gained from a relationship. Conflict may damage valuable relationships, leading to a possible loss of benefits in the future, which causes stress and motivates former opponents to reconcile. Strict dominance hierarchies lower the value of relationships within the group and thus, reduce the likelihood of reconciliation. However, the only social system for which it has been hypothesized that reconciliation would not be needed is the cooperative breeding system found among most Callitrichids. Cooperative breeders depend on each other for rearing their young. This should promote valuable relationships, but the high security of in such groups is expected to prevent any damage after conflicts. Security means that relationships are stable and predictable over time. Contrary to this hypothesis, reconciliation has been found in another species of cooperative breeders, common marmosets (*Callithrix jacchus*), but a possible link to the relationship quality of former opponents and influences of conflict characteristics have not been investigated. The current study investigated relationship quality as well as reconciliation and aimed to find out how security and value of relationships influence reconciliation. Only value seemed to influence reconciliation, as did the outcome, directionality and context of a conflict. Submissive vocalizations given by the victim after a conflict were also associated with increased reconciliation. In contrast to other studies demonstrating that valuable partners reconcile more often, no increase in self-directed behaviours indicating of stress after a conflict and their reduction after reconciliation could be found. The results show that there are dyadic differences in relationship quality in common marmosets and that these differences affect reconciliation. Nevertheless, the function of reconciliation remains unclear.

8.2.Zusammenfassung

Die Häufigkeit, mit der sich Primaten nach Konflikten versöhnen, hängt unter anderem davon ab, in welchem Sozialsystem sie leben. Je strikter die sozialen Strukturen sind, desto weniger wertvoll werden die Beziehungen sein. Wert bedeutet, dass beide Partner Vorteile durch ihre Beziehung bekommen. Durch Konflikte können wertvolle Beziehungen beschädigt werden und die Vorteile verloren gehen. Das verursacht Stress und veranlasst Gegner sich zu versöhnen. Die einzige Primatenart, in der bis dato Versöhnung nicht gefunden werden konnte, zeichnet sich durch eine kooperative Aufzucht aus. In solch einem Sozialsystem sollten Beziehungen eigentlich wertvoll sein, da die Gruppenmitglieder eng zusammenarbeiten müssen um ihre Jungtiere aufzuziehen. Die Abwesenheit von Versöhnung könnte darauf zurückzuführen sein, dass Beziehungen bei Arten mit kooperativer Aufzucht sehr sicher sind. Sicherheit bedeutet, dass eine Beziehung stabil und vorhersagbar ist. Folglich sollte auch ein Konflikt keinerlei Unsicherheit hervorrufen, wodurch Versöhnung nicht nötig wäre. Bei Weißbüschelaffen (*Callithrix jacchus*) konnte Versöhnung bereits nachgewiesen werden, allerdings wurden mögliche Zusammenhänge mit Beziehungsqualität und Konfliktcharakteristika nicht berücksichtigt. In der vorliegende Studie wurde Beziehungsqualität parallel zum Konfliktverhalten untersucht, mit dem Ziel herauszufinden, ob und wie Sicherheit und Wert Versöhnung beeinflussen. Der Wert einer Beziehung wirkte sich auf die Häufigkeit von Versöhnung aus, sowie auch der Ausgang, Kontext und die Direktionalität eines Konfliktes. Submissive Vokalisationen des Opfers nach einem Konflikt schienen Versöhnung ebenfalls zu fördern. Im Gegensatz zu anderen Studien, die einen Zusammenhang zwischen Wert und Versöhnung feststellen konnten, wurden hier allerdings kein erhöhter Stress nach Konflikten beobachtet. Die Resultate zeigen, dass Beziehungen innerhalb von Gruppen mit kooperativer Jungenaufzucht variieren und dass davon auch Versöhnung abhängt. Ob dessen Funktion tatsächlich das Reparieren wertvoller Beziehungen ist, bleibt jedoch weiterhin unklar.

8.3. Lebenslauf

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