

Peaceful Primates: The History and Function of Reconciliation in Non-Human Primate Societies

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ABSTRACT

Sociality is an important evolutionary trait that increases resource acquisition for group members while also providing protection from predators. Despite the benefits that sociality and further group living provide, group living also creates tension and conflicts between conspecifics. One method of dealing with these conflicts is through reconciliation. Reconciliation is a behavior recognized by friendly interactions between two former opponents after a conflict. Reconciliation is a unique social behavior displayed by various mammals and plays a significant role in the lives of many primate species. Reconciliation serves to reduce tension and repair important relationships between group members. The level at which reconciliation is displayed varies throughout primate species and tells an interesting story about the complex evolution of social behavior.

KEYWORDS

Primates, Reconciliation, Post Conflict Behavior, Sociality, Multi-level Selection Theory

AN INTRODUCTION TO POST CONFLICT RESOLUTION

Group living animals are often faced with developing strategies to counteract the inevitable conflicts that arise due to intra-group competition (Bernstein & Gordon, 1974). Conflicts are situations that arise when individuals behave in an observably different manner due to incompatible goals, interests, or attitudes (Aureli, Cords, & van Schaik, 2002). Conflicts create tension among members of the group, and can frequently lead to acts of aggression, which disrupt group function (Kappeler, 2002). The strategies that follow conflicts are best known as post conflict resolutions among which are three well-documented forms. These include reconciliation, *friendly conflict resolution between two opponents* (de Waal, 1979), consolation, *friendly interactions between victim and an individual that was not the aggressor* (Cordoni, 2006), and redirection, *the original victim attacks an individual that was not the aggressor* (Watts, 1995). Reconciliation is thus not the only strategy to combat intra-group competition and conflict, but it is arguably the most important for maintaining positive intra-group relationships. Reconciliation is also a topic that

has yielded a significant and consistent amount of research over the last several decades, despite the fact that only a few reviews on reconciliation exist, and nearly all of these reviews were published in or before the early 2000's. This review thus incorporates a variety of new research on primate reconciliation with our previous understanding of reconciliation function and its influences, and also makes several arguments for the evolutionary history of this behavior.

FUNCTION OF RECONCILIATION

The function of reconciliation in primates is often explained by several major hypotheses (Silk, 2002). I review these hypotheses below as well as suggest a few additional hypotheses that could potentially explain the function and evolutionary history of reconciliation later on in this paper.

Aggressive conflicts are dangerous to the individuals involved in the conflict as well as those watching (Judge, 2005). Thus at the most proximate level, reconciliation serves to reduce the likelihood of aggression following the initial conflict (Aureli, 1991). Aggressive conflicts are highly stressful for the individuals involved and acts of reconciliation act as a clear identifier that signifies the end of conflict. On a similar note, reconciliation reduces stress and anxiety for the individuals involved (Aureli, Cords, & van Schaik, 2002). This has been experimentally tested in brown lemurs (*Eulemur fulvus*) (Palagi & Norscia, 2011), captive chimpanzees (*Pan troglodytes*) (Fraser, 2010), and various other primate species (Silk, 2002).

Reconciliation also plays an important role in maintaining important social bonds and hierarchies (Cords, 1992). This has led to the development of the Valuable Relationship Hypothesis, which postulates that reconciliation should occur at higher frequencies between partners with highly valuable relationships than between those with less valuable relationships (Watts, 2006). This appears to be true in wild Japanese macaques (*Macaca fuscata*), where reconciliation occurs at significantly higher rates between dyads with a higher history or grooming relations (Majolo, 2009). This hypothesis provides an additional explanation to explain the increase of reconciliation amongst kin and friends, which is discussed at length in the section of this review titled, "Influences on Reconciliation."

A BRIEF HISTORY OF RECONCILIATION RESEARCH

Reconciliation was first defined by Frans de Waal and Marc van Roosmalen in 1979, while observing captive chimpanzees at the Arnhem Zoo in the Netherlands. Reconciliation was defined as friendly conflict resolution between former opponents, and data was gathered by following the behavior of opponents for 45 minutes after the end of a conflict (de Waal, 1979). Since this initial finding, various observational studies have been conducted to measure reconciliation in a wide variety of species and numerous changes have been made to the methodology of how such data is collected and reported (Preuschoft, 2002). Most noticeably, the duration following the end of the conflict has been significantly reduced (Kappeler, 1992). Reconciliation has also been tested in experimental settings and various

hypotheses have been developed to better understand when, how, and why primates reconcile. The bulk of reconciliation research has been conducted and published in the 90's and early 2000's. Interestingly, few review papers have been published on the study of reconciliation and new discoveries on primate reconciliation continue to be found and published at a significant rate.

ISSUES REGARDING METHODOLOGY

Despite being recognized as reconciliation, the actual behavior observed in these acts differs greatly among species and is also strongly influenced by how the researchers choose to define the act when collecting data. Among Chacma baboons (*Papio ursinus*), an important aspect of reconciliation includes soft vocalizations and grunts (Cheney, 1995). In chimpanzees reconciliation is often recognized by grooming (Webb, 2014) and in Ring-tailed lemurs (*Lemur catta*), it has been classified simply as reunions following a conflict (Roeder, 2002). In Tonkean macaques (*Macaca tonkeana*), reconciliation is identified by facial displays, mounts, and/ or clasps (Demaria, 2001). In rhesus macaques (*Macaca mulatta*), researchers measured not only reconciliation, defined as an exchange of positive signals, but also strict reconciliation, which required body contact along with positive signals in their study (de Waal & Johanowicz, 1993). Using the vague description of friendly post conflict behavior to define reconciliation thus warrants itself as a serious problem when comparing instances and patterns of reconciliation across various species.

Not only is there difficulty in defining the actual act of reconciliation, but there are also various other factors that make collecting data on instances of reconciliation challenging. A large variety of time intervals following the original conflict have been used throughout observational studies that measure reconciliation. The original study that observed reconciliation followed opposing chimpanzees for 45 minutes after the end of the original conflict (de Waal, 1979). Most studies now follow opposing members for time intervals less than 20 minutes, which may have an affect on the reported frequency of these studies (Daniel, Santos, & Cruz, 2009). This was the case in Ring-tailed lemurs who were originally thought not to reconcile after following opponents for 10 minutes (Kappeler, 1993). However, a later study followed opponents for 60 minutes and found evidence to support reconciliation in this species (Roeder, 2002). The large variety of behavioral measures used to identify primate reconciliation listed above also suggests that there are many aspects of primate communication that we are yet to understand, and this lacuna may also play a significant role in shaping our current understanding of primate reconciliation.

TAXONOMIC BREADTH OF RECONCILIATION

Reconciliation is not unique to primates, and has been found among various other mammals including goats, hyenas, dolphins, and prairie dogs and also several species of birds (Palagi, Antonacci, & Norscia, 2008). Among primates, reconciliation has been documented in over thirty primate species (Roeder, 2002),

in the wild, in captivity, and during controlled experiments (de Waal & Johanowicz, 1993). Despite this, there are also a few well-studied primate species that apparently show no signs of reconciliation including Black lemurs (*Eulemur macaco*) (Roeder, 2002). Acts of reconciliation are especially more likely to occur in Old World Primates than New World Primates, and are more frequently seen in the great apes species (Aureli, Cords, & van Schaik, 2002).

RECONCILIATION AND BYSTANDERS

The effect of conflicts on bystanders has been a more recent field of study (de Darmco, 2010). Though bystanders are generally not directly affected by instances of conflict, the period of time following aggressive behavior within a group puts all group members at increased risk of being attacked (Judge, 2005). Group members that witness aggressive attacks also have elevated levels of arousal, which is generally recognized by an increase in self-directed behavior (Maestriperieri et al., 1992). In captive Hamadryas baboons (*Papio hamadryas*), if conflicts were amended by reconciliation, instances of self-directed behavior in bystanders were reduced, suggesting that reconciliation reduces the arousal of bystanders (Judge, 2013). This evidence could also theoretically be used to argue that reconciliation has been selected for at the group level as well as the individual level.

INFLUENCES ON RECONCILIATION

There are several proposed and tested factors that are said to influence the frequency of reconciliation in primates including social influence, ontogeny, social hierarchy, conflict intensity, sex, age, individual differences, and kinship. These influences have been the subject of the majority of reconciliation research both in the past and present. Below, I list some of these said factors and provide a summary of these results in table 1. Unfortunately, studying the factors that influence reconciliation in primates is incredibly difficult because frequency of reconciliation occurs at varied rates between species and is also defined differently by various researchers (Refer to 'Issues Regarding Methodology').

I. Social Influence

Frans de Waal and Denise Johanowicz were the first to explore the relationship between social influences and rate of reconciliation (de Waal & Johanowicz, 1993). They ran an experiment in which a handful of juvenile rhesus monkeys were exposed to a group of juvenile Stumptail macaques (*Macaca arctoides*). Reconciliation is common amongst Stumptail macaques but occurs with less frequency in rhesus monkeys (Call, 1999). One set of rhesus monkeys was housed with the macaques while a control group was housed separately with only other rhesus monkeys. After 5 months of co-housing, the two rhesus monkey groups were exposed only to their conspecifics, and the experimental group was found to have a 30% increase in likelihood of reconciliation following conflicts (de Waal & Johanowicz, 1993). Results like these could theoretically be used to suggest

the idea that reconciliation may be an important aspect of primate culture, which could have its own selective advantages, though to my knowledge no current literature exists that has meshed these two ideas together (Jablonka & Lamb, 2005).

II. Ontogeny and Developmental Influences

Reconciliation is also affected by the quality of mother offspring relationships, at least in captive brown capuchins (*Cebus apella*). Under the assumption that infant behavior during times of distress is highly influenced by mother offspring relationships (Spanglar, 1994), Ann Weaver and F.B. de Waal were able to experimentally find evidence to support that infants with secure mother offspring relationships engaged in conflicts less often than insecure infants and that when they did engage in conflict the likelihood of reconciliation was far greater than that of infants with insecure mother offspring relationships (Weaver & de Waal, 2003). On the other hand, rhesus macaques that generally display moderately high levels of reconciliation will refuse to reconcile if raised in solitude without other conspecifics (Kempes, 2009). This further suggests that the primary facilitator of reconciliation is through cultural and not genetic means.

III. Social Hierarchy

Social hierarchy has also been a proposed influence on reconciliation, as pigtailed macaques of lower social rank were found to reconcile with higher ranking conspecifics more frequently than equal or lower ranking conspecifics (Judge, 1991). This has been noted in a variety of species including Pigtailed macaques (*Macaca nemestrina*) and White sifakas (*Propithecus verreauxi*) (Palagi, Antonacci, & Norscia, 2008). This is also consistent with the Valuable Relationships Hypothesis, as lower ranking individuals should value their relationships with higher-ranking conspecifics at greater levels than equal or lower ranking conspecifics.

IV. Intensity, Result, and Details of Conflict

The intensity of the conflict is similarly thought to influence reconciliation frequency, but various studies have found no correlation in many primate species including olive baboons (*Papio anubis*) and stumptailed macaques (Castles, 1998; Call, 1999). Conflict intensity is also generally influenced by various other factors, thus even if such influence was found it would be difficult to interpret. The end result of the conflict is often an important aspect that influences reconciliation. Conflicts in Japanese macaques that end with increased uncertainty are more likely to be reconciled (Aureli et al., 1993; Castles, 1998; Silk 2002). If the conflict was initiated due to some sort of dispute while foraging, primates rarely reconcile (Aureli, 1992). This is either because the act of foraging delays reconciliation to a later time or that the individuals are more concerned with foraging than making up after the conflict.

V. Sex, Age, and Individual Differences

Age has been found to have no influence on likelihood of reconciliation in neither long tailed macaques (*Macaca fascicularis*) (Cords, 1992), nor stumptailed macaques as well (Call, 1999). Sex has been speculated as an influence on reconciliation too and varies greatly between species given the differences in group gender composition. Sex was also found not to influence reconciliation in long tailed

macaques (Cords, 1992) and stumptailed macaques either (Call, 1999), or white sifakas (Palagi, Antonacci, & Norscia, 2008), but was found to be highly influential in captive gorillas (*Gorilla beringei*) (Cordoni, 2006). Specifically in this group, female-male reconciliation occurred most frequently followed shortly by female-female, and male-male instances of reconciliation were found to very rarely occur (Cordoni, 2006). A similar pattern was found among captive bonobos (*Pan paniscus*) (Palagi, Paoli, & Tarli, 2004). More recently, researchers have begun to measure the influence that individual differences have in affecting the rate of reconciliation. In 2014, a link between rate of reconciliation and social switching behavior in chimpanzees was found in captivity. This research suggests that chimpanzees that display higher rates of reconciliation also show higher rates of switching between various social states (Webb, 2014). This evidence should not be particularly surprising as the very nature of reconciliation calls for two individuals that were competing opponents to engage in friendly non aggressive behavior in a relatively short period of time following some sort of conflict.

VI. Kinship

One of the most influential aspects that affects occurrences of reconciliation is kinship. Though this varies tremendously at the species level, generally all research suggests an increase in rate of reconciliation among kin. In stumptailed macaques, kinship and friendship were found to be the only factors that influenced rates of reconciliation; factors such as sex, age, rank, conflict intensity, outcome, or number of participants were controlled and accounted for (Call, 1999). Kin bias affecting rates of reconciliation has also been observed in rhesus monkeys (Call, 1996), captive gorillas (Cordoni, 2006, Watts, 1995 [ii]) wild barbary macaques (*Macaca sylvanus*) (McFarland, 2011), captive chimpanzees (Koski, Koops, & Sterck, 2007) and wild Japanese macaques (Majolo et al., 2009). This has been linked to the close relative proximity that kin tend to maintain after a conflict as well as the Valuable Relationship Hypothesis (Call, 1996 & Watts, 2006). These findings support the notion of reconciliation being used as an effective way to repair important social bonds. These findings are also useful in understanding the evolutionary history of reconciliation, as possibly being selected on via the means of kin selection (Hamilton, 1964), though I argue in the closing section that there are additional evolutionary hypotheses to explain the existence of reconciliation.

Table 1.
Influences on Reconciliation Observed in Non-Human Primates

Proposed Influence	Species	Source	Has an Effect (Y/N)
Social Influence	Rhesus Monkeys	(de Waal & Johanowicz 1993)	Yes
Ontogeny	Captive Brown Capuchin	(Weaver & de Waal 2003)	Yes
Ontogeny	Rhesus Macaque	(Kempes et al. 2009)	Yes

Hierarchy/Rank	Pigtailed Macaque	(Judge 1991)	Yes
Hierarchy/Rank	White Sifaka	(Palagi, Antonacci, & Norscia 2008)	Yes
Conflict Intensity	Olive Baboons	(Castles & Whiten 1998)	No
Conflict Intensity	Stumptailed Macaque	(Call, Aureli, & de Waal 1999)	No
Conflict Ending	Japanese Macaque	(Aureli et al. 1993 & Castles 1998)	Yes
Reason for Conflict	Long Tailed Macaque	(Aureli 1992)	Yes
Age	Long Tailed Macaque	(Cords 1992)	No
Age	Stumptailed Macaque	(Call, Aureli, & de Waal 1999)	No
Sex	Long Tailed Macaque	(Cords 1992)	No
Sex	Stumptailed Macaque	(Call, Aureli, & de Waal 1999)	No
Sex	Captive Gorilla	(Cordoni, Palagi, & Tarli 2006)	Yes
Sex	Captive Bonobos	(Palagi, Paoli, & Tarli 2004)	Yes
Sex	White Sifaka	(Palagi, Antonacci, & Norscia 2008)	No
Individual Differences	Captive Chimpanzees	(Webb et al. 2014)	Yes
Kinship	Stumptailed Macaque	(Call, Aureli, & de Waal 1999)	Yes
Kinship	Rhesus Monkeys	(Call 1996)	Yes
Kinship	Captive Gorilla	(Cordoni, Palagi, & Tarli 2006)	Yes
Kinship	Barbary Macaque	(McFarland & Bonaventura 2011)	Yes
Kinship	Captive Chimpanzees	(Koski, Koops, & Sterck 2007)	Yes
Kinship	Japanese Macaque	(Majolo et al. 2009)	Yes

Note: Table 1 Lists some of the various influences on reconciliation that have been proposed and tested on wide variety of non-human primate species in recent literature. All species were observed in the wild unless marked "captive" in the species column.

EVOLUTIONARY HISTORY AND AN ARGUMENT FOR GROUP SELECTION

So far, I have made the case for two proximate functions of reconciliation; stress reduction and maintaining social bonds. The aspect of stress reduction is certainly understandable via 'natural selection reasoning,' and the same case can

be made for maintaining social bonds. The reported kin bias also shown in some species (Call, 1999, reference Table 1) also supports the notion of reconciliation being acted on by kin selection theory (Hamilton, 1964).

I believe an argument can also be made to explain the selection of reconciliation at the group level. As shown in D.S. Wilson's 1975 model, the selection of altruistic traits can be favored at the group level, even while reducing the fitness of the individual (Wilson, 1975). While there are clear benefits to an individual performing acts of reconciliation, there are also various risks involved with the behavior as well. These risks include receiving further aggression from the original individual in conflict or from other individuals in the group (Aureli, Cords, & van Schaik, 2002; McFarland, 2011). Despite these risks, the occurrence of reconciliation in so many species (including non-human primates) suggests that it is a crucial mechanism in maintaining the function of social groups (Aureli, 1997; de Waal, 2000; Koyama, 2006; Weaver & de Waal, 2003). Reconciliation also benefits the bystanders of the conflict (see section labeled 'Reconciliation and Bystanders') further suggesting that this is a behavior that is adaptive at the group level. It is thus important to acknowledge that though reconciliation is advantageous to the individual, groups that display reconciliation will do better than groups that do not, therefore these groups will be selected for at a higher level of selection.

As evolutionists, it is of course, difficult to empirically determine the causes and specific selective pressures that have led to the current phenotypic traits of interest. This task is only made more difficult by the fact that researchers have limited knowledge regarding the evolution of human behavior, and even less on the behavior of other primate species. However, if groups of primates that frequently displayed acts of reconciliation were more cooperative with each other, and were consequently able to outperform competing groups, we would expect to see the selection of reconciliation at the group level, which may explain its widespread existence.

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