# 5 Something to make peace for: conflict management and resolution

*Man is neither, by nature, peaceful nor warlike. Some conditions lead to war, others do not.*

Otterbein 1997, p. 272

## 5.1 The end of social groups

After the death of King Alfonso XI of Castile in 1350, his eldest son Peter took control of the territory. Peter's mother, Maria of Portugal, had Alfonso's mistress, Eleanor de Guzman, killed. The death of Eleanor, who had given birth to ten children (Peter's half-siblings) split the royal descendants (legitimate and illegitimate) into two rival factions: Peter and his allies, and Alfonso's children by Eleanor, the Trastámaras, led by Henry. In the fights over the territory, Peter defeated the coalition led by his half-brother Henry in 1356 and 1360 and had two half-brothers (Henry's full brothers John and Peter) executed. Henry was forced to flee but later gained the support of Aragon, France, and many nobles of Castile. Meanwhile, Peter allied with Edward, heir to the English throne. This alliance allowed Peter to maintain the control upon the territory, until when Edward fell ill and, for political reasons, withdrew his support to Peter. Eventually, Henry took over the territory as Henry II and was responsible for the death of his half-brother Peter. John II, the great-grandson of Henry II, came to power after his mother Catherine of Lancaster, the regent, died in 1418. John II lacked authority and the territory became a battlefield for the nobles, more or less related to the ruling family, to gain power. As a result, the Trastámara family was, again, divided into two main factions: John II (with his supporting nobles) and his cousin Alfonso V of Aragon with his allies and brothers, Henry and John. In 1420, John II was kidnapped by his cousin Henry and then liberated by an ally, Álvaro de Luna. In 1429, Alfonso V ordered his brothers Henry and John to lead a joint attack (which was unsuccessful) against their cousin John II. In 1443 John II was once again captured by his cousin John of Aragon and the territory fell into near anarchy until 1445, when the group of nobles supporting John II, led by Álvaro de Luna, won a battle and Henry of Aragon was killed. When in 1454 Henry IV succeeded John II, another internal rift divided the royal family, with part of the nobles sustaining Henry IV's daughter Joan as a legitimate successor and another part sustaining Henry IV's half-brother Alfonso and, after his strange premature death in 1465, his half-sister Isabel. Isabel, who married Ferdinand (the heir to the throne of Aragon), eventually took over the territory

but in the process her original family had been completely destroyed (for further information: Valdeón Baruque, 2002; Jardin, 2015).

As stressed by Otterbein (1997), 'some conditions lead to war, others do not'. War and unmanaged violence under certain circumstances may not be convenient for the preservation of social groups. For example, raiding of neighbouring groups was a common custom in the Tandroy people, traditional warrior-pastoralists living in south Madagascar and organised in clans (Jolly, 2004). However, the endless wars over cattle, land, women, tributes and succession, in which military alliances were forever changing, led to the disruption of Tandroy groups and, consequently, of their culture. Besides the cases reported above, human history is full of examples of the annihilation of entire families or groups to obtain power, such as the internal fighting among the pharaoh's descendants in ancient Egypt (e.g., Merneptah's heirs in the nineteenth dynasty), the famous War of the Roses in the England of the fifteenth century and described by Shakespeare in his first historical tetralogy, or today's Mafia blood feuds.

Lemur 'history' is also rich in episodes of internal family and group fighting to control a territory. As a matter of fact, lemurs often live in groups in which many individuals are more or less tightly related to one another. Group fission, enhanced by the death of the dominant female or by the increase of troop size, involves active targeting by the dominant clique of a subordinate clique (Jolly, 2012). Subordinates, once forced out, can fight to establish new territory by subdividing the original home range, or fight to take neighbouring troops' ranges (Koyama, 1991; Jolly et al., 1993; Hood and Jolly, 1995; Koyama et al., 2002; Takahata et al., 2005; Ichino, 2006; Ichino and Koyama, 2006; Jolly et al., 2006; Jolly, 2012).

Soma and Koyama (2013) reported that in a troop of Berenty ring-tailed lemurs, when the 'matriarch' died, a fight started among her descendants. The troop was originally composed of the descendants of one dominant female, the 'grandmother'. The grandmother and her second daughter died between December 2003 and August 2004. After the death of the grandmother, hierarchy stability crumbled and the group started reorganising. The second daughter's daughters (orphans) formed a subgroup. The fourth youngest daughter formed a subgroup with her most compliant younger sisters, ultimately depriving her older sisters of their high ranks. In fact, she became the alpha female. The oldest sister, now beta-ranked, formed another subgroup with her two sons. The middle-ranked sister associated, instead, with her subadult son. Therefore, four subgroups rose after the death of the matriarch: the dominant female and her younger sisters, the beta-ranked sister's family, the middle-ranked sister's family, and the subgroup of orphan daughters. In October 2014, the dominant female (after having offspring) and her subgroup chased away – via repeated target aggression – two of their nieces, from the orphan subgroup. The expulsion process started after one of the two nieces had delivered an infant. Eventually, the two nieces ran away, crossing the territories of two other troops, and they could never come back. After the eviction, whenever the alpha female and her younger sisters encountered the expelled nieces they pursued them aggressively. Instead, the subgroups of the

older aunts did not. By September 2005, the evicted nieces had gained a sleeping site on the boundary of the territories of two other groups. However, they did not often win confrontations with other troops. One of the expelled nieces dropped her infant while retreating from a confrontation in October 2014. By the end of October the nieces had not yet succeeded in establishing their own territory and on 31 October 2005, their male consort was found dead from unidentified causes. A further example of lemur conflict is the so-called 'Civil War' reported by Alison Jolly (2004) in another troop of Berenty ring-tailed lemurs. During the 1992 drought, the group led by Diva drove the subordinate half of the group away. For several weeks the exiles ran across the ranges of at least five neighbouring troops and could feed only when no other group was around. During the repeated and exhausting confrontations with the original group, two of the exiled females lost their babies following two events of infanticide perpetrated by an immigrant male, in one case, and by a female from the original group in the other case. The evicted subgroup kept losing the contests with the original group until the exiled females changed their battle tactic. Instead of leaving just a couple of animals in the 'fire front' they started presenting a united front. The evicted subgroup started winning confrontations, taking over more and more feeding trees, thus getting to control the best and widest part of the territory. Hence the original, defeated group became marginalised and after the death of the alpha female included only a small number of individuals. In 1997, the alpha female of the fallen group, facing shrinkage of territory and food resources, chased away the daughter of the former alpha female with her little group (her daughter, her niece and their offspring). In this case the newly evicted subgroup did not succeed in conquering its own space within the original home range and its members died or disappeared one by one. By using the word 'war' Alison Jolly underlined how complex the fight tactics can be, even in lemurs, and stressed how the changing coalitions are crucial in determining the outcome of social conflicts.

In chimpanzees, the most famous case of conflict is the 'Four Year War of Gombe chimpanzees', reported by Jane Goodall in the 1970s. The seed of the conflict was planted when the so-called Kasekela community began to split. Seven adult males and three mothers and their offspring began spending most of their time in the southern part of the community's home range. By 1972, these chimpanzees had formed their own group, known as Kahama. When the males of the two communities met each other in the overlapping zone, they engaged in typical territorial fights. Then, a series of deadly brutal attacks perpetrated by the Kasekela members on the individuals of the Kahama community followed, leading to the annihilation of Kahama (Goodall *et al.*, 1979; Goodall and Berman, 2000). The coalitionary killing of chimpanzees was then observed in many study sites other than Gombe (Tai National Park, Ivory Coast: Boesch and Boesch-Achermann, 2000; Kibale, Uganda: Watts and Mitani, 2000; Muller, 2002; Watts *et al.*, 2006; Budongo, Uganda: Newton-Fischer, 2002; Loango, Gabon: Boesch *et al.*, 2006; Mahale, Tanzania: Kaburu *et al.*, 2013).

In the past, conflicts in chimpanzees have been used to make an argument in favour of the biological nature of human violence and in support of the evolutionary

vision of human warfare as derived from chimpanzee-like conflicts. But when new pieces of evidence started accumulating on bonobos (*Pan paniscus*), the African ape at least as close to humans as chimpanzees, the 'warrior vision' started creaking. Bonobos have never been observed engaging in coalitionary killing and, in contrast to chimpanzees, show higher levels of cooperation in problem solving and tolerance (de Waal and Aureli, 1996; Hare *et al.*, 2012) related to more socially symmetrical relationships (de Waal, 1987; Fruth and Hohmann, 2002; Palagi and Cordoni, 2012), male–female co-dominance (Palagi *et al.*, 2006; Box 4.1), developmental delay with respect to social play (Paoli *et al.*, 2007; Palagi and Cordoni, 2012) and non-conceptive sociosexual behaviour (Koski and Sterck, 2009; Rilling *et al.*, 2012). Additionally, compared to chimpanzees, bonobos seem to possess a greater amount of grey matter in the brain regions involved in perceiving others' distress, an emotional state underpinning empathic abilities (Call *et al.*, 2002). Based on these characteristics, some scholars consider bonobos as a better model than chimpanzees to make inferences about the behaviour of extinct and extant hominids (Fry, 2012). For example, it has been reported that ancestral hominid conflict behaviour may have been more bonobo- than chimpanzee-like (de Waal, 2009), as suggested by the small, non-projecting canines and reduced sexual dimorphism of 4.4-million old *Ardipithecus ramidus* (White *et al.*, 2009; Fry 2012). The new pieces of information, added up, draw a different scenario in which humans and their predecessors were more likely prey than hunters (Hart and Sussman, 2011). Different from 'chimpanzeeists', 'bonobists' theorise that humans are not biologically deemed to violence and war.

In an interview on the BBC website, Dr Bostrom from Oxford University's Future of Humanity Institute stated that 'We're at the level of infants in moral responsibility, but with the technological capability of adults. There is a bottleneck in human history. The human condition is going to change. It could be that we end in a catastrophe or that we are transformed by taking much greater control over our biology.' (www.bbc.com/news/business-22002530). The fact that culture can somehow help us control our biology recalls Huxley's vision of the garden and the gardener, according to which ethics and human nature (the garden) need the continuous intervention of intelligence and culture (the gardener) to be maintained (Huxley, 1893). With today's knowledge, we know that culture comes from the brain, which is one of the most wonderful and marvellous products of biological evolution. Therefore, the dichotomy between culture and biology, and the idea that war is the result of thoughtless human biology whereas its control is the result of cultural intervention, have no foundation any more. Biology itself provides the tools to limit aggression and imposes the control of it because massive disruptive behaviours would prevent the survival of social groups thus proving anti-adaptive, unless group viability is jeopardised. When resources are limited the only exit strategy allowing the survival of at least part of the population may be group disruption. On one hand, the reduction of group size can restore environmental viability (with fewer animals accessing resources in a given area); on the other hand the formation of different 'factions' can increase the risk of violent intergroup fights to gain exclusive

control over resources. The new social settings generated by the conflict are usually unstable and may require uneasy adjustments. Splitting can ultimately exacerbate group fragmentation, leading to the annihilation of the smallest subgroups if not of a significant part of the population. Given the costs of group disruption (see the examples of humans, chimpanzees and lemurs described above), the possible future gains resulting from engaging in a war must be extremely high and likely. This improbable condition makes the disruptive conflict the last resort to rely on.

To preserve their integrity, social groups adopt conflict management strategies that can be handled in many ways, with only a few of these actually involving physical violence (Rubin *et al.*, 1994; Fry, 2006). In humans, with variation from one culture to the next, disputants, for example, may seek the help of an impartial mediator to resolve their disagreements, negotiate a form of compensation, practice avoidance or decide to make peace without any form of intervention or compensation (Fry, 2012). These types of conflict management which for many years have been associated with the human cultural background are strategies that are in place, also in other animal species.

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Box 5.1 | **by Cary J. Roseth**

**Speaking of which: peacemaking in children**

My interest in children's conflict resolution began as a teacher at a boarding school for 14- to 18-year-old students. Like many new educators, I started teaching with the assumption that I would have some 'good' students and some, let's say, 'less good' students. My hope was to help these less good students change their ways and become knowledgeable, well behaved, and other-oriented adults.

Of course, what I quickly realised is that students are both good and less good, and that different social contexts elicit different kinds of behaviour. These insights may seem trivial to ethologists, but most teachers rarely see their students outside of class and, as a result, tend to have a one-dimensional view of their students. As a boarding school teacher, however, I saw my students many times a day in multiple settings, and in so doing gained a much more complete understanding of their behavioural repertoire. Much to my surprise, even my good students exhibited selfish behaviours, and even 'anti-social' behaviours like aggression proved adaptive under some circumstances.

Unlike ethologists, teachers also tend to focus on improvement and reform rather than objective behavioural analysis. For peer conflict, this means that teachers are keenly aware of the costs that conflict may impose on society, especially if conflict involves physical aggression. However, at boarding school, I had the opportunity to view peer conflicts from start to finish, and in so doing learned to appreciate the variety of antecedents and consequents associated with these events. I learned that 'hitting' was not simply a 'behaviour intended to harm another', which is the typical definition of aggression

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in the psychological literature, nor was 'hitting' always indicative of social incompetence. Instead, hitting and other aspects of peer conflict could not be fully understood outside the social and behavioural context in which they were embedded.

In sum, what fascinated me as a young teacher about children's conflict is the same thing that continues to fascinate me today. Understanding peer conflict and its resolution demands that we reconsider common assumptions about what constitutes right and wrong behaviour and what constitutes social competence. The subject's biological roots also demand that conflict and its resolution be examined at multiple levels of analysis. Indeed, there is no end to the questions that can be asked about its immediate causation, development, function and evolution.

One of the most interesting findings from our research is the extent to which preschoolers – children 3 to 5 years old – actively balance their own self-interests with those of others. What makes this so interesting is that it contrasts so fundamentally with psychologists' historical assumption that children are developmentally self-centred and thus unable to understand others' perspectives, much less act in a way that balances their interests with those of others.

Indeed, our research has shown that preschoolers behave strategically in conflict situations, even using aggressive behaviour in functionally suitable ways. In fact, preschoolers use both *coercive* (e.g., aggression, threats) and *prosocial* behaviours (e.g., cooperation, affiliation) to control resources, and those preschoolers who use both of these strategies – so-called 'bistrategic' resource controllers – enjoy privileged access to both agentic and communal resources such as peer regard, attention and affiliation. Our research also shows that preschoolers tend to use costly coercive strategies (e.g., physical aggression) to establish resource control when peer relationships are new or unstable (Pellegrini *et al.*, 2007; Roseth *et al.*, 2007, 2011), less costly coercive (e.g., verbal aggression) and prosocial strategies (e.g., prosociality) to maintain resource control when peer relationships stabilise (Roseth *et al.*, 2007), and a combination of coercive and prosocial strategies as well as reconciliation to offset potential social costs and foster affiliation (Roseth *et al.*, 2011). Another one of our interesting findings is that the frequency of preschoolers' conflict is curvilinear, increasing then decreasing in accord with the stability of peer relationships (Roseth *et al.*, 2007, 2011). This finding indicates that bistrategic resource control involves more than using both coercive and prosocial strategies some of the time, and instead involves careful calibration, with preschoolers matching both the form and combination of strategies to the context in which resource control bouts occur (see also Pellegrini *et al.*, 2011a, b). Here again, these findings challenge traditional views of social

Box 5.1 (continued)

Box 5.1 (*cont*.)

competence and what 'counts' as prosocial and antisocial behaviour. These findings also challenge the common assumption that all forms of aggression are indicative of social-cognitive deficits, suggesting instead that some forms of aggression may actually encourage the development of children's conflict resolution.

Perhaps most surprising, we have also found that teacher intervention during preschoolers' peer conflict may inhibit natural conflict resolution. In fact, preschoolers are more likely to stay together and resume friendly interaction when teachers do *not* intervene during coercive bouts (Roseth *et al*., 2008). What makes this surprising of course is that most teachers intervene in children's conflict with the intent of helping them to develop constructive means of resolving conflict. Rather than improve and reform children's conflict resolution, however, our findings suggest that teacher intervention may actually disrupt children's developing abilities.

Research on children's conflict and its resolution is at its infancy now, as little is known about biological determinants, developmental trends, cognitive and sociocognitive correlates, and the way socialisation affects form and function. Future research is also needed to examine how children learn to calibrate personal and social concerns, and the extent to which such calibrations depend on their status within different social hierarchies. We also know very little about the role of children's empathic responses to others' harm and vulnerability, and whether these responses motivate reconciliation or third-party intervention.

Finally, future research is needed to examine conflict resolution in other age groups and in other settings. While the preschool years offer a unique window into the emergence of conflict resolution, the setting also represents the human equivalent of captive animal research. In fact, many university preschools are described as child development 'laboratories' and are outfitted with one-way glass, observation booths and cameras. Such amenities support careful observation data collection, of course, but are hardly representative of a 'natural habitat'. Future research is therefore also needed to examine conflict resolution in the home and among older children in a variety of social settings.

## 5.2    Aggressive behaviour: from the individual-centred to the relational perspective

Violence is more prominent than harmony. In the media, a single case of aggression (towards family, friends, spouse, etc.) garners more attention than many incidents of cooperative behaviour enacted to prevent aggression from occurring or to buffer its consequences. The scenario drawn from the media (joined to a good dose of

readers' insane curiosity) has contributed to bias people's perception towards the feeling that we live in a violence-grounded society. Violence is unquestionably present in social settings but it is hard to believe that human social life is governed by violence. What makes the news on severe violence so striking is that it is more unusual than the positive interactions normally characterising everyday life, leading to conflict prevention and resolution.

For decades after the start of the first ethological studies, aggressive behaviour has been defined as antisocial, regardless of whether it was considered an innate, pre-programmed behaviour (Lorenz, 1966: hydraulic model) or the result of both instinct and experience (Tinbergen, 1968). In such studies, the antisocial character of the aggressive behaviour was biased by the model species, the setting, or the experimental protocol selected to study the effect of agonistic events. For example, in different species, spanning rats and humans, aggression was studied in experimentally isolated individuals and was often induced through painful stimulation (Johnson, 1972). This unnatural setting strongly altered the behavioural response of animals, preventing them from engaging in any form of regulation of the aggression.

Zuckerman in his book of 1932 (*The Social Life of Monkeys and Apes*) concluded that monkey society was based on and ruled by aggression because he had observed that two-thirds of his study group of hamadryas (*Papio hamadryas*) had been exterminated by internal fights, started by males to take possession of females. De Waal (1989a) argued that this tremendous situation derived from a condition of severe crowding (more than 70 animals were kept in a 20 × 30 m enclosure) and extremely imbalanced sex ratio, since only a few females were present in the group. These conditions, which would be stressful for any social species, proved unsustainable for hamadryas, whose society is organised in one-male units (or harems: one reproductive male with several reproductive females). Again, the totally artificial and aberrant conditions prevented the possibility for Zuckerman's animals to adopt tactics of conflict management.

Studies on highly territorial and solitary animals were used as another source of data to support the antisocial nature of aggression. Indeed, some fish and bird species use conflicts to keep intruders away and secure the exclusive use of resources in an area (de Waal, 1996; de Waal *et al.*, 2000). When animals do not know each other, aggression is used to maintain distance and leads to dispersal (individual model; de Waal *et al.*, 2000). Clearly, in this context, animals compete for resources without getting back any benefit from group living, such as lower risk of predation, better ability to defend food resources, and information sharing on food, competitors or predator location. But does it really make sense talking about antisocial behaviour when the social setting is missing?

When animals coexist in social groups, conflicts of interest are common because several or many individuals share the same territory and find themselves competing for the same resources. For example, the presence of a desirable resource (food item, oestrus female, shelter, etc.) can tickle the appetite of different group members, thus leading to a conflict between the individuals interested in such resource. Yet, social living has been positively selected in many animal species. Therefore, social animals

must have found a way to manage conflicts of interest, avoiding the disruption of their group. In the social context, stating that aggression is an antisocial behaviour is just not correct. First of all, a fight requires the interaction between at least two individuals, the actor and the receiver of the aggression. Moreover, aggression can be one of the very elements upon which social cohesion is grounded. The dominance hierarchy of social groups is established via aggressive events. The outcome of such events, determining winners and losers, allows animals to acquire different ranking positions. In the long run, the rise and maintenance of a hierarchy based upon previous aggression limit future aggression. By knowing their own place in the hierarchy, animals can choose to stay away from each other, with an individual, typically a subordinate, withdrawing from trying to access a resource, in order to avoid dangerous competition with a dominant. The subordinate animal has to make a decision on the basis of the costs and benefits of engaging in overt competition with a dominant. When rank differences between individuals are high, starting a fight with a powerful group member is likely to be a lost cause. Consequently, the resource automatically goes to the dominant and the risk of receiving an aggression (and being injured) is warded off. This tactic of avoidance is used to work out a conflict of interest (by simply dropping competition) in an alternative to aggression. In short, aggression regulates aggression via a negative feedback cycle.

The avoidance tactic can be also used when, by limiting social interactions, animals can reduce the probability that a conflict of interest arises in the first place. This situation has been observed in groups of apes kept under limited space conditions (Cordoni and Palagi, 2007), where no emergency exit is available and when the rise of conflicts over food, preferred locations, etc. is highly probable. The reduction of animals' activity, known as the elevator effect (de Waal *et al.*, 2000), allows avoiding severe aggression, which could have disastrous outcomes in an enclosure with no escape opportunities. Also in this case, experience of previous aggression occurring under high-density conditions helps mould avoidance tactics and, therefore, the hypothesis that past aggression may serve to limit future aggression still stands.

Besides avoidance, an individual can tolerate another over a resource, possibly sharing part of it or letting a group mate access it, in exchange for future cooperation (coalitionary support, territory defence, food search, etc.). The level of tolerance can vary according to the species considered (more or less despotic), the quality and quantity of the resource, and the behavioural mechanisms adopted by animals to buffer social tension when a conflict of interest can be foreseen (pre-conflict strategy). As will be discussed in Part III, such mechanisms can involve play, grooming, and other types of affinitive contacts, which can enhance tolerance towards others.

Sometimes aggression is inevitable but animals cannot afford to let aggression destroy their social group every time that a conflict of interest comes along. Hence, mechanisms to resolve the conflicts have been developed to fix the social relationships damaged by aggressive events. The most basic form of conflict resolution is reconciliation, occurring when former opponents directly engage in post-conflict reunion through friendly contacts, more technically defined as affinitive interactions.

It is possible to talk about reconciliation only when two individuals engage in affinitive contacts most frequently after they have fought. Otherwise, friendly contacts could be simply part of the usual interactions the former opponents engage in, and not enhanced by the conflict and used to buffer its negative consequences.

Reconciliation represents the 'formal act' promptly and unequivocally settling the hostility between former opponents and restoring their relationship. Individual recognition and memory of previous aggressive events are the only items of the 'cognitive equipment' that animals need to reconcile. Due to its low cognitive cost, reconciliation is probably the most powerful mechanism that many species of social animals can use to avoid the disruption of their group. Literature has confirmed that post-conflict reunion occurs in different species of corvids (Clayton and Emery, 2007; Fraser and Bugnyar, 2010, 2011) and across mammals, from gregarious marsupials (Cordoni and Norscia, 2014) to highly social primates (Fry, 2013). Besides reconciliation, other more sophisticated mechanisms can be adopted by social animals (including humans, see Box 5.1 above). Third parties not involved in the conflict can mediate the reunion of the two opponents by contacting either the victim or the aggressor (see Box 5.2 to further explore this aspect), also depending on the quality of the relationship binding the third party and each one of the opponents. In this case, higher relational cognitive abilities are required since animals must somehow 'understand' their social position in the group and the relationship linking the other group members to one another. However, the debate over the abilities that animals need to engage in third-party interactions and their actual significance (consolation, appeasement, protection, aggression buffering, etc.) is totally open.

Avoidance, tolerance and aggression (followed or not by reconciliation) are the three pillars of the Relational Model proposed by de Waal (2000) to explain how conflicts of interest can be managed in social animals.

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Box 5.2  |  **by Giada Cordoni**

**Speaking of which: conflict management in non-primate mammals**

Competition and aggressiveness are customarily presented as the natural state of affairs in the animal kingdom (human society included) (Koenig, 2002; Rubenstein, 2012; Thierry, 2013). Conflict management is a pool of behavioural strategies which are fundamental for the maintenance of group integrity (Aureli and de Waal, 2000). Therefore, we expect to find them wherever and whenever a social group is in place. These strategies include reconciliation between opponents (de Waal and van Roosmalen, 1979), triadic affinitive contacts directed towards victim or aggressor (Palagi *et al.*, 2004, 2006; Cordoni *et al.*, 2006; Koski and Sterck, 2007) and quadratic affiliation among bystanders (Judge and Mullen, 2005; Leone *et al.*, 2010). Starting from the pioneering study on chimpanzees by de Waal and van Roosmalen (1979),

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Box 5.2 (*cont.*)

numerous studies have demonstrated the occurrence of natural conflict resolution in many primate species (Aureli *et al.*, 2002). Nevertheless, demonstrating the occurrence of post-conflict behaviours is not enough to unveil the role of such behaviours in group maintenance and social relationship establishment. Several studies have been carried out in non-primate mammals (domestic goat – Schino, 1998; spotted hyena – Wahaj *et al.*, 2001; bottlenose dolphin – Weaver, 2003; domestic dog – Cools *et al.*, 2008). By using a comparative approach, these studies underlined the differences and similarities with primates in aggression management. For example, in domestic goats, post-conflict friendly reunions can play an important role in reducing the victim's anxiety; similar findings were reported in long-tailed macaques as well (Aureli and van Schaik, 1991). Studying non-primate species can help in determining the potentially diverging roles of different post-conflict strategies.

I started investigating and comparing different features of reconciliation and third-party affiliations (e.g., frequency, timing, modality) in two non-primate species, the red-necked wallaby (*Macropus rufogriseus*) and the grey wolf (*Canis lupus lupus*).

Notwithstanding the divergence between Metatheria and Eutheria mammals that occurred some 168–178 million years ago (Luo *et al.*, 2011; dos Reis *et al.*, 2012), marsupials have evolved many morphological, behavioural and neocortical traits that are markedly comparable to those of placental mammals that occupy similar niches (Karlen and Krubitzer, 2007; Meredith *et al.*, 2008; Isler, 2011). It is possible to hypothesise that evolution has led marsupial and placental mammals to develop similar solutions to deal with similar social challenges, such as competition and aggressiveness.

Contrary to other marsupials, red-necked wallabies are gregarious and face the challenges of spatial closeness, including coexistence around feeding sites. The occurrence of reconciliation found in this species (mean group corrected conciliatory tendency: 27.40%; Cordoni and Norscia, 2014) supports the hypothesis that, like other social or gregarious placental mammals facing similar pressures, wallabies enact post-conflict strategies to reduce possible negative consequences of a conflict.

As in the great apes (Arnold and Whiten, 2001; Aureli and Schaffner, 2002; Fraser *et al.*, 2008) and two prosimian species, *Propithecus verreauxi* (Palagi *et al.*, 2008a) and *Lemur catta* (Kappeler, 1993), conciliatory contacts between wallabies can play an important role in limiting the likelihood of further attacks towards the victim by the aggressor and in reducing the rates of post-conflict scratching in both the opponents, functioning as an anxiety reliever (Arnold and Aureli, 2007) and, consequently, as a social uncertainty reductive mechanism (Uncertainty Reduction Hypothesis, Aureli and van Schaik, 1991). After an aggression, the temporary interruption of partner

compatibility (Cords and Aureli, 2000) may endanger the ordinary social associations and the degree of interindividual tolerance in both opponents, thus causing anxiety. Red-necked wallabies maintain their interindividual relationships via continuous 'covert' interactions, such as social sniffing, social licking, feeding in contact and scent marking (Higginbottom and Croft, 1999; Jarman, 2000). Therefore, also in this species reconciliation may represent a useful tool to restore relaxed social conditions.

Moving from marsupial to placental mammals, my interest focused on a highly social and cooperative species, the grey wolf (*Canis lupus lupus*). The typical wolf pack is structured as a family group including a breeding alpha pair and its offspring (Mech and Boitani, 2003; Miklósi, 2014). In a pack, individuals generally form a well-established linear hierarchy in which all males dominate over all females (Mech, 1999; Cordoni and Palagi, 2008). My colleague Elisabetta Palagi and I demonstrated the occurrence of reconciliation (Cordoni and Palagi, 2008) and third-party affiliations (Palagi and Cordoni, 2009; Cordoni and Palagi, 2015), directed both towards the victim (victim triadic affiliation) and the aggressor (aggressor triadic affiliation), in grey wolves.

According to the Valuable Relationship Hypothesis (Kappeler and van Schaik, 1992; Cords, 1997; van Schaik and Aureli, 2000), in wolves the frequency of reconciliation was affected by the coalitionary support rates: the higher the levels of exchange support, the higher the rates of reconciliation. This result fits with the features of wolf social life. In fact, despite the strict hierarchical arrangement of individuals, the pack existence and integrity strongly rely on cooperation between fellows, which have specific roles and act in a flexible way, following environmental and social changes (Peterson *et al.*, 2002). A similar result was obtained in Assam macaques (*Macaca assamensis*) where the females reconciled more with individuals with whom they exchanged more agonistic support, which increases the probability to access resources and to maintain the social status (Cooper *et al.*, 2005).

Through the investigation of triadic post-conflict affiliations (towards either victim or aggressor), other functional similarities between primates and wolves have been demonstrated. In *Canis lupus lupus*, similar levels of victim triadic affiliation (mean group triadic contact tendency: 63.27%) and aggressor triadic affiliation (mean group triadic contact tendency: 44.78%) were found, although the two types of triadic post-conflict affiliations showed a functional dichotomy (Palagi and Cordoni, 2009; Cordoni and Palagi, 2015). Victim triadic affiliation reduces the likelihood of renewed attacks towards the victim as predicted by the Victim Protection Hypothesis, already demonstrated in bonobos (Palagi and Norscia, 2013) and chimpanzees (Palagi *et al.*, 2014). On the other hand, aggressor triadic affiliation decreases the probability of renewed attacks

Box 5.2 (continued)

Box 5.2 (*cont.*)

towards uninvolved third parties by reducing the arousal of the aggressor as predicted by the Appeasement Hypothesis (*sensu* van Hooff, 1967). Studies on chimpanzees (Romero *et al.*, 2011) and lowland gorillas (Palagi *et al.*, 2008b) have shown a similar function of aggressor triadic affiliation.

In wolves victim triadic affiliation occurred more frequently in the absence of reconciliation, functioning as a substitute for conciliatory contacts between opponents (Substitute for Reconciliation Hypothesis) as found in many primate species (e.g., chimpanzees, Palagi *et al.*, 2006; Fraser and Aureli, 2008; bonobos, Palagi *et al.* 2004; baboons, Wittig *et al.*, 2007; mandrills, Schino and Marini, 2012; monkeys, Palagi *et al.*, 2014a). Aggressor triadic affiliation tended to be more likely after the occurrence of reconciliation thus suggesting that contacting an aggressor immediately after conciliatory contacts reduced the risk for the bystander to be the object of a renewed attack. The interdependency of reconciliation and aggressor triadic affiliation in primates is still under debate. In chimpanzees, Romero *et al.* (2011) found that aggressor triadic affiliation occurred more often in the absence of reconciliation whereas in the same species Koski and Sterck (2007) found no support for the Substitute for Reconciliation Hypothesis.

The study on wolves has demonstrated that victim triadic affiliation and aggressor triadic affiliation represent the two sides of the same coin: affiliation with the aggressor is distributed according to the individual ranking position and support value, thus highlighting the strict hierarchy characterising wolf society; at the same time, affiliation with the victim is affected by the strength of the relationship quality, thus underlying the cooperative aspect of the wolf social system.

Contrasting victim and aggressor triadic affiliations concurrently in the same social group provides the opportunity to understand the precise role of each of the two behavioural categories. Surprisingly, in primates the victim and aggressor triadic affiliations have never been examined at the same time, although natural conflict resolution has been studied in primates more than in any other taxon. This is an interesting line of research that I would like seen addressed in the future.

## 5.3   Give peace a chance: reconciliation and lemurs

### Pre-conflict mechanisms

Different behavioural mechanisms can be used to reduce conflict probability in social groups. The affinitive contacts adopted by group mates to reduce the likelihood of aggression in stressful conditions, such as the contacts occurring right before food distribution or in crowding conditions, depend on the species behavioural repertoire. Humans can use language, songs, symbolic gestures and friendly

contacts such as handshakes, embraces, nose rubbing and kisses to increase tolerance (Firth, 1972; Kendon and Ferber, 1973; de Waal, 1989a; Floyd 1999, 2001; Field, 2014; daily news and…look around). Gorillas – which are not renowned for their proclivity to engage in intense affiliative interactions (Harcourt, 1979; Watts, 1995, 1996) – have been observed touching each other more often in response to greater density (Cordoni and Palagi, 2007). In this case, touch is a rapid affiliative item selectively used across the different sex–class combinations as appeasement behaviour (Cordoni and Palagi, 2007). The exuberant bonobos, which contrary to gorillas enjoy the pleasure of vigorous social contacts, cope with stressful conditions by selectively increasing grooming, play and the frequency of non-reproductive sexual interactions (Palagi *et al.*, 2006; Paoli *et al.*, 2007; Tacconi and Palagi, 2009). Chimpanzees, other than increasing grooming, use greetings such as kissing and submissive bowing as an aggression disclaimer (de Waal, 2000; Palagi *et al.*, 2004).

In monkeys, grooming is the most relevant behaviour to increase tolerance (for further information on grooming see also Chapter 8). The highly despotic rhesus macaques seem to cope with crowded conditions by grooming each other more frequently. Males groom other males and females more frequently under limited space conditions, with a consequent reduction of aggression rates (Judge and de Waal, 1997; de Waal, 2000).

Spider monkeys (*Ateles geoffroyi*) show aggressive escalation during subgroup fusion events. During these events, animals embrace each other more often thus mitigating aggression. In this case, embraces (but not grooming) appear to be effective in appeasing or reassuring others (Aureli and Schaffner, 2007). In capuchin monkeys, grooming has been found to serve as a conflict prevention mechanism. Before scheduled feeding, a predictable competitive situation, grooming rates increase and the risk of aggressive escalation decreases (Polizzi di Sorrentino *et al.*, 2010).

Grooming also seems to work in reducing the probability of aggression in strepsirrhines, even if the data available in this respect are meagre.

In red-fronted lemurs, low-ranking females exchange grooming for the tolerance of dominant females. In fact, subordinate females have been observed giving the largest amount of grooming (relative to what they received) to high-ranking females probably to reduce the risk of being evicted from their group (Port *et al.*, 2009). In general, the higher the level of grooming asymmetry (grooming given versus grooming received), the higher the frequency of aggression observed. This is consistent with previous findings on wedge-capped capuchin monkeys showing that equal reciprocation of grooming time between partners characterises affiliative grooming relationships to strengthen social bonds and reduce the probability of aggression (O'Brien, 1993). These results highlight the long-term relationship between grooming reciprocity within dyads and the probability of agonistic events (Port *et al.*, 2009).

Overall, the mechanisms of conflict prevention in lemurs have been largely neglected, if not completely ignored. Indeed, finding appropriate literature to draft this chapter has not been easy at all. This is why at this point we decided to stop writing and start analysing unprocessed data in order to fill part of the gap.
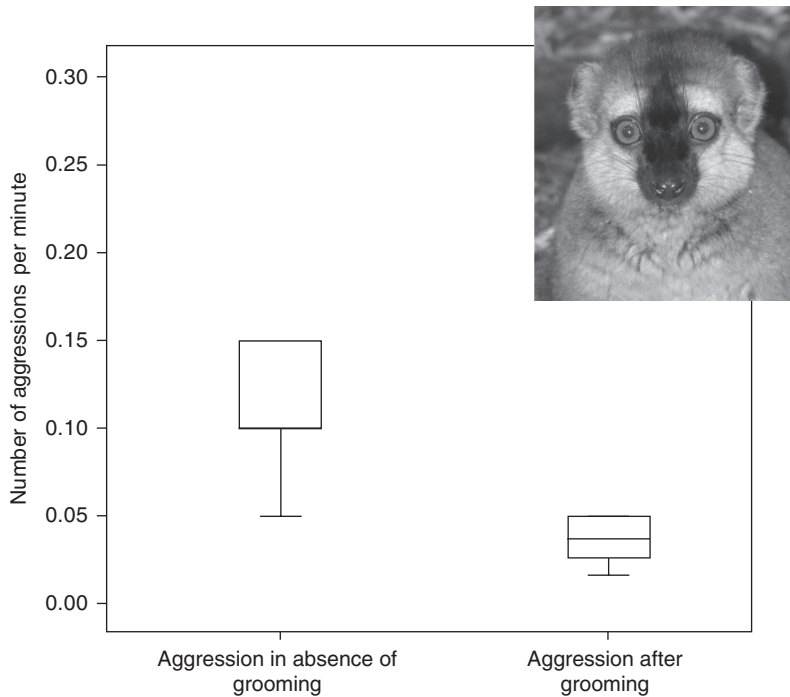
**Figure 5.1** Frequency of aggressive events that occurred in presence and absence of previous grooming interactions in *Eulemur rufus* × *collaris* from the Berenty forest, Madagascar. Exact Wilcoxon's test: T = 0, ties = 0, n = 8, *p* < 0.05. Photo: Elisabetta Palagi.

By scrutinising our records on lemurs from the Berenty forest, collected from 2006 to 2011, we verified if it was less likely that two individuals engaged in aggressive interactions after being involved in a grooming session. We focused on the possible cause–effect relationship existing between the occurrence of grooming and subsequent aggression. Within focal sampling periods of ten minutes, we observed that grooming significantly reduced the probability of aggression involving the former groomer and groomee in *Eulemur rufus* x *collaris*, *Propithecus verreauxi* and *Lemur catta* (Figures 5.1, 5.2 and 5.3). These results confirm that also in the short term, grooming can be a pre-conflict tool employed by lemurs to limit the occurrence of aggression. This is a coping strategy in that tolerance levels are raised by increasing affiliation rates.

*Lemur catta* seems able to deal with the possible devastating effect of violent conflicts under space reduction. To verify the effect of reduced space availability in lemurs, we analysed the data collected in the period 2004–2005 in captive lemurs hosted at the Pistoia Zoo (Tuscany, Italy). Here, the lemurs could stay in a grassy yard outside (100 m²) or in an inside enclosure (20 m²). To reduce the biases related to seasonality we restricted the analyses to those months when both conditions (inside and outside) were present. Data were gathered over 119 hours inside and 67 hours outside. When comparing the agonistic events (normalised over the hours of observation) occurring in the
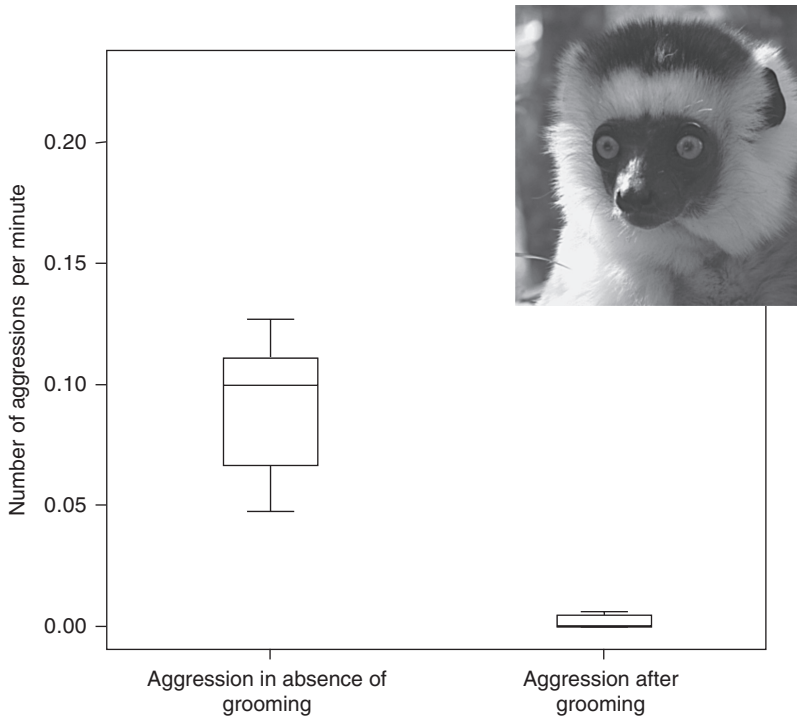
**Figure 5.2** Frequency of aggressive events that occurred in presence and absence of previous grooming interactions in *Propithecus verreauxi* from the Berenty forest, Madagascar. Exact Wilcoxon's test: T = 1.00, ties = 1, n = 14, *p* < 0.001. Photo: Ivan Norscia.
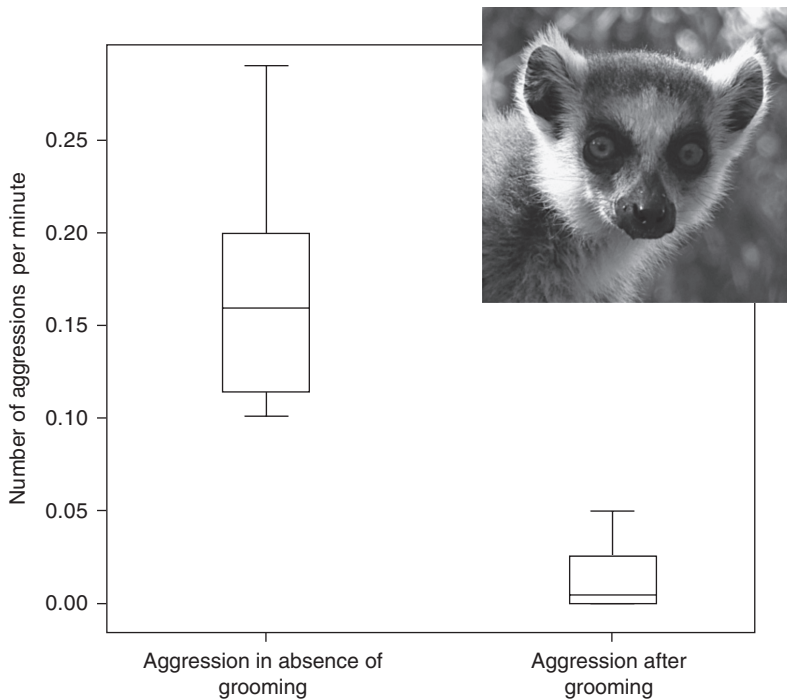


**Figure 5.3** Frequency of aggressive events that occurred in presence and absence of previous grooming interactions in *Lemur catta* from the Berenty forest, Madagascar. Exact Wilcoxon's test: T = 0, ties = 0, n = 10, *p* < 0.01. Photo: Elisabetta Palagi.

outside enclosure with those occurring in the inside room, we found that the overall level of agonistic events did not differ between the two conditions;[1] nor did grooming.[2] Yet, lemurs were able to limit aggressive incidents of high intensity, involving chasing, bite and grab bouts (*sensu* Palagi *et al.*, 2005). In fact, the proportion of severe conflicts over the total number of aggressive events was significantly reduced when animals were hosted inside, under short-term crowding conditions.[3] Therefore, under brief crowding periods, dominants do not appear to control the quantity of their attacks but their modality, making them less intense and therefore less dangerous. Even if we considered the lemur species characterised by the most despotic social structure (*Lemur catta*, see also Chapter 4), our results do not support the density–aggression model, predicting that high-density conditions lead to higher levels of aggression (Calhoun, 1962). Instead, the tactic put in place by ring-tailed lemurs to avoid the escalation of aggressive encounters is consistent with the coping model, predicting that animals can respond to crowded conditions by modifying their behaviour to reduce the number and/or severity of aggressive encounters (de Waal, 1989b; Aureli and de Waal, 1997; Judge and de Waal, 1997; de Waal *et al.*, 2000; Judge, 2000).

The 'elevator effect' described by de Waal and coworkers (2000) predicts that individuals finding themselves in confined spaces tend to inhibit their activity in order to avoid conflicting interactions. This paradigm is consistent with our results on captive lemurs which, once again, express tactic abilities also observed in monkeys and apes. For example, capuchin monkeys significantly reduce intense aggression, play and social grooming when spatially confined, thus limiting social encounters. A clear signal of the elevator effect is that under acute crowding capuchins increase self-grooming, which reduces arousal and does not implicate any social interaction (van Wolkenten *et al.,* 2006). Adult gorillas have been observed avoiding interactions under space reduction by staying more spatially dispersed and increasing the levels of sitting alone, avoidance, and dismissing behaviours (Cordoni and Palagi, 2007).

Another behaviour used by lemurs to prevent conflicts from occurring is play. The linkage between social play and aggressive contacts is particularly evident in captive ring-tailed lemurs. For example, those dyads showing low aggression rates can engage most frequently in play fighting (Palagi, 2009). While analysing the behavioural sequences of play fighting in juvenile ring-tailed lemurs, Pellis and Pellis (1997) found that play dynamics strongly resembled those of real aggression. In many primate and non-primate species, the roughness of play fighting can likely lead to the escalation into serious fighting (Fagen, 1981; Pellis, 2002a). However, the low levels of aggression found in ring-tailed lemurs under playful contexts (Palagi, 2009) suggest that animals are able to cope with possible ambiguous and dangerous situations. In this view, play can be considered as a tool to increase tolerance and, at the same time, to assess own and others' physical and social skills

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[1] Overall aggression rates did not differ between outdoor and indoor conditions (Exact Wilcoxon's test: n = 9, T = 19.00, $p$ = 0.734).

[2] Overall grooming frequencies did not differ between outdoor and indoor conditions (Exact Wilcoxon's test: n = 9, T = 10.00, $p$ = 0.164).

[3] The proportion of high-intensity conflicts over the total number of aggressive occurrences was lower indoors than outdoors (Exact Wilcoxon's test: n = 9, T = 3.00, $p$ = 0.039).

in a safe context. The potential of play in relaxing social interactions and increasing tolerance is reinforced by playful signals such as relaxed open mouth (Palagi *et al.*, 2014a), body postures and movements (Palagi, 2009; Yanagi and Berman, 2014), which can modulate the intensity of the interaction and increase the fairness between the playmates.

In a species characterised by a high level of social tolerance, the Verreaux's sifaka, play is used by adult males as an ice-breaker mechanism, thus establishing the conditions to accept new adult males in the social group during the mating season, a period of high conflict of interest (Antonacci *et al.*, 2010). Play is used not only by lemurs but also by many other primate taxa (and not exclusively to increase tolerance), as extensively explained in Chapter 7.

## Post-conflict mechanisms

As already discussed earlier in this chapter, despite the existence of several mechanisms to avoid aggression, sometimes the conflict is inevitable because the wanted resource is crucial and inalienable or because there are not the conditions to employ pre-conflict buffering measures. Once the aggression has occurred it is necessary to engage in post-conflict affiliative interactions, such as reconciliation (Figure 5.4), to restore the relationship between former opponents and avoid negative consequences (e.g., conflict spreading) for the entire social group. The occurrence of reconciliation – defined as the first exchange of affiliative contact between opponents soon after a conflict (de Waal and van Roosmalen, 1979) – has been found in humans (Fujisawa *et al.*, 2005; Box 5.1) and other social or gregarious mammals (e.g., wallabies, Cordoni and Norscia, 2014; domestic goats, Schino, 1998; horses, Cozzi *et al.*, 2010, spotted hyenas, Wahaj *et al.*, 2001; wolves, Cordoni and Palagi, 2008; domestic dogs, Cools *et al.*, 2008; dolphins, Weaver, 2003; primates, Aureli *et al.*, 2002; see also Box 5.2).

Within primates, this kind of conflict resolution has been extensively studied in monkeys and apes but much more rarely in strepsirrhines (Figure 5.5). Yet, comparing social strepshirrhines with the best-known anthropoids is crucial for a better understanding of the evolution of conflict resolution mechanisms. Alison Jolly stressed the importance of comparative studies as the key to understand in depth the dynamics of lemur social behaviour. Based on early studies she pointed out that 'ringtailed lemur interactions are much more black and white than in many anthropoids – either affiliative or aggressive – between any two animals, with minimal ambiguity, and no reconciliation after quarrels...Reconciliation has recently been asserted for sifaka, ringtails and brown lemurs, using different measurements....Complexity of social relations would be worth revisiting by someone very familiar with behavior of both monkeys and prosimians' (Jolly, 2012, p. 33).

As explained in the preface to this volume, lemurs (which retain ancestral traits such as a small brain and communication highly based on smell) contrast with anthropoids in various behavioural features, including female dominance, lack of pronounced sexual dimorphism and strict seasonal breeding (Martin, 1990; Wright, 1999). However, group-living lemurs share basic features with anthropoids such as

**Figure 5.4** Tail anointing in *Lemur catta* male. His ears are flattened, which preludes a ritualised or real fight (top). *Propithecus verreauxi* during grooming, one of the most common affinitive patterns used by primates to reconcile (bottom). Berenty forest, Madagascar. Photos: Ivan Norscia and Elisabetta Palagi.
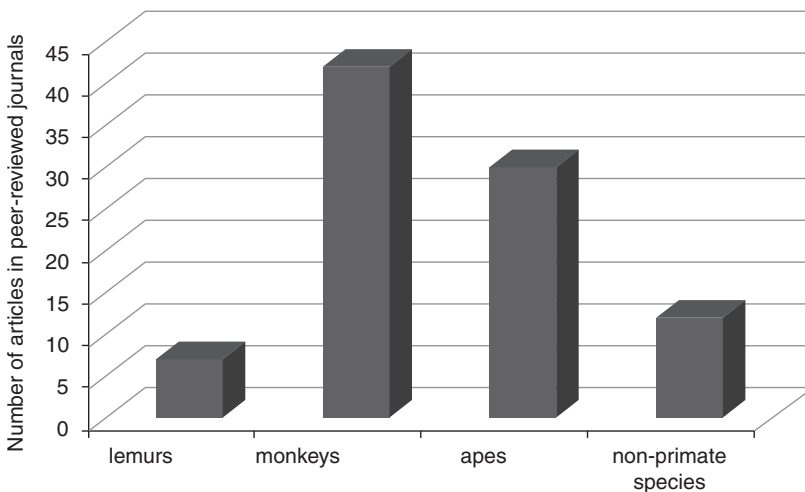


**Figure 5.5** Scientific articles on natural conflict resolutions published in peer-reviewed journals up to February 2013.

cohesive multimale/multifemale societies, female philopatry (Pereira and Kappeler, 1997) and individual recognition (Palagi and Dapporto, 2006, 2007), a prerequisite for reconciliation (Aureli *et al.*, 2002).

Despite the importance of extending conflict management studies to strepsirrhines, until 2008 post-conflict behaviour had been investigated only in a handful captive groups of lemurs: *Eulemur fulvus*, *Eulemur macaco*, *Lemur catta* (Kappeler, 1993; Rolland and Roeder, 2000; Roeder *et al.*, 2002; Palagi *et al.*, 2005). Later, the investigation was extended to wild lemurs (*Propithecus verreauxi*, Palagi *et al.*, 2008a; *Eulemur rufus × collaris*, Norscia and Palagi, 2011; Palagi and Norscia, 2015). In 1993, Kappeler had predicted that the occurrence of reconciliation could be linked to the levels of tolerance of social groups because he had found reconciliation to be present in *E. fulvus* but not in *L. catta*, with the latter being characterised by the highest levels of despotism. The subsequent studies have confirmed this hypothesis. In fact, reconciliation was not found in *Eulemur macaco* (Roeder *et al.*, 2002) and in the majority of groups of *Lemur catta* in which the phenomenon had been investigated (Kappeler, 1993; Palagi *et al.*, 2005). *Eulemur macaco*, compared to *Eulemur fulvus*, shows despotic female dominance (Roeder *et al.,* 2002; Hemelrijk *et al.*, 2008). Studies in the wild have confirmed that in more tolerant species, namely *Propithecus verreauxi* and *Eulemur rufus × collaris,* reconciliation is present. Therefore, the presence of reconciliation in *P. verreauxi* suggests that this species, characterised by relaxed interindividual relationships, is more similar to *E. fulvus* (also showing looser hierarchical relationships) than to *L. catta* and *E. macaco*, at least in terms of dominance style. In social strepsirrhines, the occurrence of reconciliation, scattered across different taxonomic groups, depends on the dominance style of the societies, more than on the phylogenetic closeness of the species. Something similar has been observed in 20 different *Macaca* species, which share similar social organisation (multimale-multifemale) but which largely diverge in the dominance style. In macaques, a positive correlation was found between the degree of group tolerance and the level of reconciliation (Thierry, 1986, 2000; de Waal and Luttrell, 1989). For example, reconciliation rates are higher in the tolerant Tonkean (*Macaca tonkeana*; Thierry, 1985a, b; Petit and Thierry, 1994; Demaria and Thierry, 2001; Ciani *et al.*, 2012; Palagi *et al.*, 2014a) and crested macaques (*Macaca nigra*; Petit *et al.*, 1997) than in the despotic Japanese macaques (*Macaca fuscata*; Chaffin *et al.*, 1995; Schino *et al.*, 2004).

According to the Social Constraints Hypothesis (de Waal and Aureli, 1996) the differences in primate social styles (de Waal and Luttrell, 1989), already present in infancy (Thierry, 1985a), influence a wide range of behaviours including aggression, affiliation, dominance and nepotism (Thierry, 1985b, 1990; Aureli *et al.*, 1997; Petit *et al.*, 1997; Balasubramaniam *et al.*, 2012). The studies on lemurs have revealed that in strepsirrhines, as in haplorrhines, peacemaking is not only possible but also shaped by similar social variables. Hence, the Social Constraints Hypothesis largely confirmed in monkeys and apes (de Waal and Aureli, 1996) applies to strepsirrhines, as well.

It is hard to determine whether the similar distribution of reconciliation according to the social style found in both strepsirrhines and haplorrhines is an evolutionary

analogy or homology. The forces driving the reconciliation phenomenon have probably been in place since the origin of the primate group but the entity of the phenomenon likely depends on whether social groups have acquired (or not acquired) a certain dominance style. The cost-benefit ratio, as predicted by the basic sociobiology theories (Wilson, 2000), determines if taking the risk of reconciling is worth it or not. Considering the presence of reconciliation as the simple aftermath of the dominance style would be reductive. Beyond primates, high rates of reconciliation have been found in wolves (*Canis lupus*; mean conciliatory tendency, 44.1% in the wild: Baan *et al.*, 2014; 53.3% in captivity: Cordoni and Palagi, 2008). Within a pack, every subject knows its social standing with every other individual and each group defends its own territory as a unit. Yet, even if the alpha male normally guides the movements of the pack and initiates aggressions against intruders (Mech, 1977), the subordinate members can sometimes oppose their leader's actions. According to Zimen (1981), no subject decides alone the carrying out of activities that are vital to the group cohesion. In short, wolves are highly despotic but also extremely cooperative, to the point that bystanders can conveniently affiliate with either aggressors or their victims depending on the situations (Cordoni and Palagi, 2015; Box 5.2). The existence of an extremely cooperative pack has presumably to do not only with hunting but also with the collective rearing of offspring and, consequently, with reproductive success (Mech and Boitani, 2003). It is clear that in wolves the benefit of reconciling and preserving the social bonds outweighs the cost deriving from pack disruption, which would be detrimental for both dominants and subordinates. Thus, reconciliation can be found in despotic groups provided that they are cooperative. Further evidence of this assumption is the presence of reconciliation in spotted hyenas (*Crocuta crocuta*). Hyenas are despotic but often depend on help from other group members during hunts, defence of ungulate carcasses against competitors, and coalition formation that is important in both the acquisition and maintenance of social rank (Wahaj *et al.*, 2001). In hyenas, as in wolves, the necessity to cooperate overcomes the competition between dominants and subordinates, which explains the presence of reconciliation. The lower levels of reconciliation observed in hyenas (mean conciliatory tendency: 11.3%) may be due to the fact that, contrary to wolves, spotted hyenas live in a fission–fusion society allowing dispersal – other than reconciliation – as an exit strategy.

Cooperation and despotism are two opposite forces that contribute in shaping reconciliation patterns, in a number of species, including lemurs. When the balance between these forces strongly fluctuates according to seasonal variations, long-term studies are needed in order to unveil reconciliation, especially if occurring at low frequencies. This is the case of *Lemur catta*, a species considered as virtually unable to reconcile. However despotic *Lemur catta* may be, female–female coalitionary support is present, especially during aggressive interactions. Therefore, reconciliation can play a role also in this species. Consistently, the phenomenon was present in one captive group hosted at the Pistoia Zoo, Italy and two wild groups from the Berenty forest, Madagascar (Palagi and Norscia, 2015). The presence of reconciliation could be detected thanks to the extensive database available, which allowed
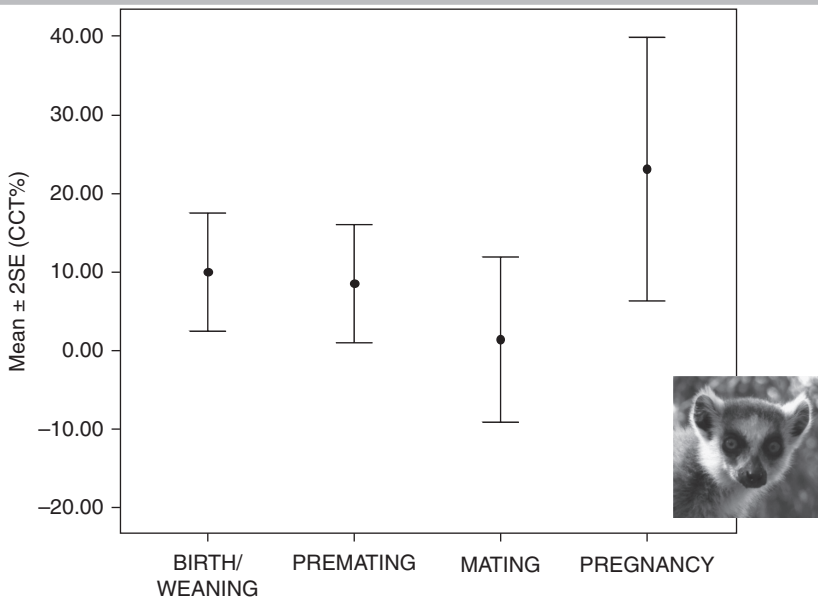
**Figure 5.6** Seasonal fluctuation of corrected conciliatory tendencies (CCTs) in *Lemur catta*. Reconciliation rates are minimum during the mating period (Palagi and Norscia, 2015), thus the period in which data are collected is crucial to highlight the presence of the phenomenon. Photo: Elisabetta Palagi.

analysis of 2339 post-conflict (PCs) and matched control (MCs) focal observations collected from eight groups, five in the wild and three in captivity.[4] We found that the season, more than other variables (wild/captivity setting, rank or individual features), influenced the reconciliation levels, which were lowest during the mating period (Figure 5.6). This result is consistent with the strict reproductive seasonality of *Lemur catta*, in which female oestrus lasts around one day per year. Overall, it is confirmed that reconciliation can be present in a despotic species but not when the advantages of intragroup cooperation are annihilated by intragroup competition, as it occurs in seasonal breeders when reproduction is at stake.

In lemur species characterised by lower levels of despotism, the phenomenon of reconciliation seems to have a more prominent role in the maintenance of group homeostasis. In *Propithecus verreauxi* and in *Eulemur rufus* × *collaris*, the conciliatory tendency can reach high levels (Verreaux's sifaka: mean 44.72% ±6.51 SE; brown lemurs: mean 26.62% ±8.34 SE) and reconciliation could be detected over

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[4] After the last aggressive pattern of any given agonistic event, the loser of the interaction was followed as the focal individual for a ten minute post-conflict period (PC). Matched control observations (ten minute long MCs) took place during the next possible day at the same time, context (feeding, resting or travelling) and physiological season (lactation, pre-mating, mating, and pregnancy) as the original PC. The MC was conducted on the same focal animal, in the absence of agonistic interactions during the ten minutes before the beginning of the MC and when the opponents had the opportunity to interact. For further details on the methods used for this study case see Palagi and Norscia, 2015. For details on the general methodology see for example: de Waal and Yoshihara, 1983 (original article) and Aureli and de Waal, 2000 (extensive review).

short observation periods. Nevertheless, also in these species reconciliation remains linked to cooperation/competition balance. In fact, reconciliation did not reach any significant level when the aggression occurred in the feeding context (Palagi *et al.*, 2008a; Norscia and Palagi, 2011), when (again) a crucial resource is at stake and competition higher. Therefore, in lemurs as in other primates, reconciliation can be influenced by season or context and be subject to the evaluation of costs and benefits, which in turn depends on whether cooperating is more rewarding than competing. This theoretical concept found an empiric support in *Propithecus verreauxi*. In this species, victims were found more likely to engage in post-conflict affiliation with the former aggressor after low-intensity agonistic encounters occurred outside the feeding context. Moreover, lemurs were more likely to reconcile with valuable partners: post-conflict affiliations were preferentially initiated by subordinates with top-ranking individuals, and occurred more frequently between animals sharing good relationships. Hence, lemurs can evaluate possible risks and benefits before engaging in post-conflict reunions, in order to gain long-term benefits such as future cooperation. In *P. verreauxi*, reconciliation was also found to reduce – in the short term – the probability of further attacks on the victim by the same aggressor (Palagi *et al.*, 2008a). In this respect, reconciliation may be seen as an *hic-et-nunc* mechanism,[5] needed to avoid conflict spreading across group members, possibly leading to social disruption. While a similar short-term function of reconciliation was found in *Eulemur rufus* × *collaris,* the strategic use of reconciliation as a tool to gain possible long-term benefits was not detected in this species. Here, reconciliation was not biased towards valuable or high-ranking group mates (Norscia and Palagi, 2011).

Reconciliation offers a further example of the importance of investigating phenomena by applying a comparative approach not only to strepsirrhines and haplorrhines but also within strepsirrhines themselves. Lemur species (and groups!) characterised by differences in the interindividual relationships, social looseness and hierarchical steepness (see Chapter 4 for reference) can provide different elements to understand the proximate and ultimate factors underlying the evolution of important behavioural phenomena, such as conflict management and resolution.

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Box 5.3 | **by Peter Verbeek**

**Speaking of which: the contribution of peace ethology to life science**

I came to the study of aggressive and peaceful behaviour from a broad interest in social behaviour. Social behaviour is a fascinating topic of study to me because it involves interactions between actors with potentially diverging interests. How will social actors work out inevitable conflicts of interest? Do they opt for dealing with it aggressively or peacefully? And what factors

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[5] *Hic et nunc* means 'here and now', a mechanism that works in the same moment in which the action is enacted.

affect their choice of strategy? Seeking answers to these kinds of questions got me started in this field and still motivates my work today.

The main purpose of life on Earth as we understand it is to sustain and propagate itself. I want to know the role that peaceful behaviour plays in sustaining and propagating life across the entire spectrum of life, including the human manifestation of it. The notion that human beings occupy a pinnacle position on this Earth, somehow removed in behaviour and mind from nature, has never made sense to me. I agree with psychiatrist and environmentalist Ian McCallum that 'strictly speaking, there is no such thing as human nature. There is only nature and the very human expression of it' (McCallum, 2012). Doing comparative research on aggressive and peaceful behaviour in multiple species, including my own, feels natural to me. Moreover, I am convinced that the comparative method is indispensable if we want to uncover the very human expression of aggression and peace (cf. Tinbergen, 1968; see also Verbeek, 2008, 2013).

Most valuable to me are findings or insights that help me plot a new course for my work. The findings from my own work and that of my colleagues that show that across cultures young children can make peace with peers without adult intervention is a good example of that (Butovskaya *et al.*, 2000; Verbeek and de Waal, 2001; cf. Kempes, 2008). The fact that in timing, form and function, early peacemaking in our own species resembles not only that of our primate cousins (Silk, 2002; Verbeek 2008), but also that of several other mammal species (e.g., Cordoni and Palagi, 2008), and even some birds (e.g., Fraser and Bugnyar, 2011), is shaping my research and thoughts about the future of the field as a whole. My research on aggression is teaching me the importance of the distinction between species-typical and species-atypical aggression (Verbeek *et al.*, 2007; cf. Haller and Kruk, 2006). Recent findings that show that peaceful behaviour can also be species-typical or species-atypical (e.g., Sapolksy, 2006, 2013) have inspired me to pursue the distinction between species-typical and species-atypical in both aspects of my research.

I foresee an exciting and productive future for this research domain as it evolves from the study of natural conflict resolution (Aureli and de Waal, 2000) into a comprehensive study of peaceful behaviour. Now that we are finally looking at it systematically and comprehensively, it turns out that peaceful behaviour, such as friendly cooperation, helping and sharing, and behaviours that keep aggression in check, or re-establish non-violent relations and tolerance following conflict, appears in a wide range of species. Intriguing new findings such as sharing and peacekeeping in colonial orb web spiders (Wenseleers *et al.*, 2013), increased cooperation among more distant relatives in species ranging from eusocial insects (van Zweden *et al.*, 2012) to cichlid fish (Stiver *et al.*, 2005), and the policing of selfish behaviour in

Box 5.3 (continued)

Box 5.3 (*cont.*)

genetically identical ants (Oldroyd, 2013), all clearly illustrate that explaining how and why peaceful behaviour has evolved and persists across a wide range of species now counts among the greatest challenges for behavioural biology. I see three interrelated ways in which the research domain will most likely develop and expand. First, as mentioned earlier, I expect that the field of natural conflict resolution will develop into a comprehensive peace ethology (Verbeek, 2008, 2013). Second, I foresee an important role for such a behavioural biology of peace in the future development of life science as a whole. Third, I expect that peace ethology will become one of the key disciplines within an emerging multidisciplinary behavioural science of peace. I discuss each of these three future directions next.

**Peace ethology.** In the final chapter of their epoch-making volume *Natural Conflict Resolution*, Filippo Aureli and Frans de Waal list eight research questions for which they felt answers were specifically needed (Aureli and de Waal, 2000, pp. 375–379). Four of these questions address ultimate concerns (species-comparisons on natural conflict resolution, including human vs non-human, functional questions, and links to the evolution of morality and justice), while four address proximate concerns (health, development, peacekeeping and social structure) (cf. Tinbergen, 1963).

*Natural Conflict Resolution* effectively translated Niko Tinbergen's ideas about an ethological approach to 'War and peace in animals and man' (Tinbergen, 1968) into testable research questions and integrative goals. However, at the time the volume was published, behavioural biology had become conceptually and institutionally divided (Thierry, 2007). Ethologists were mainly interested in behavioural mechanisms and behavioural development (i.e., proximate concerns; Kappeler *et al.*, 2013), while the study of the evolution and function of behaviour had been all but claimed by behavioural ecologists (i.e., ultimate concerns; Kappeler *et al.*, 2013). Now, 13 years after the publication of *Natural Conflict Resolution*, and 50 years after Tinbergen's seminal 'On Aims and Methods of Ethology', (Tinbergen, 1963) the ethological approach to social behaviour that effectively integrates ultimate and proximate considerations is making a strong comeback (Kappeler *et al.*, 2013; cf. Blumstein *et al.*, 2010). The stage appears set for a behavioural biology of peace that does full justice to the vision and expectations of its pioneers.

**Peace ethology's expected contributions to life science.** I believe that understanding the interplay between aggressive and peaceful behaviour is fundamental to understanding life. I predict that following contemporary life science's recent quantitative successes (e.g., genomics; molecular biology) new breakthroughs in our understanding of life will be more qualitative in nature. I expect that new holistic approaches will shed light on

mutually beneficial interdependencies in life on Earth (Scofield and Margulis, 2012), including those between microbiomes and genomes, as expressed, for example, through behaviour (Ezenwa *et al.*, 2012) and development (Pennisi, 2013). New findings on mutualisms and interdependencies in nature will revitalise life science, and I predict that research on obstacles and catalysts of peaceful behaviour will make significant contributions to this, in particular through the coming of age of a genuine peace ethology.

**Peace ethology's expected contributions to a multidisciplinary behavioural science of peace.** There are compelling reasons for a translational multidisciplinary behavioural science of peace. While seeking sustainable development solutions will be a key goal for present and future generations, 'The most important public good is peace' (Sustainable Development Solutions Network, 2013, pp. 26). Like health, peace is a requirement for human happiness and well-being. Unlike health, of which we understand many of the physical and mental processes, our understanding of the processes of peace and what sustains them are still limited (cf. Coleman and Deutsch, 2012). Our knowledge of health derives for a great part from the fact that we routinely look beyond the human condition towards the rest of nature for an understanding of what impedes or optimises our health. A mature peace ethology can lead the way in doing the same for peace.

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