"The body of my enemy": Armed conflicts in societies without wealth
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Intergroup interactions and conflicts in non-human primates: mechanisms and evolutionary pathways toward warfare

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Abstract: The question of the origin of human warfare has triggered much debate and conjecture. The study of intergroup conflicts in our closest living relatives, the non-human primates, allows to dispassionately address this question from an evolutionary perspective. Primatology research reveals the proximate and ultimate mechanisms at work in primate intergroup conflicts, which can be extremely variable. Here, we review these mechanisms, highlighting the socio-ecological conditions leading to an intensification of intergroup conflicts, such as resource distribution, population density, group composition and familiarity. The concept of intergroup dominance and the associated fitness benefits demonstrate that intergroup competition for territories and their resources motivates inter-group conflicts. However, individual motivations to participate undermine the efficiency and coordination of collective action, creating collective action problems. In contrast, chimpanzee territorial behaviour implies group-level cooperation, but also a pronounced hostility toward out-group members. The imbalance of power explains the occurrence of intergroup killings in chimpanzees, and the parochial cooperation model, proposing that strong social ties cement group-level actions, explains to co-occurrence of cooperation and out-group hostility. Intergroup conflicts can then act as a selective pressure favouring in-group cooperation. Intergroup conflicts can escalate to violent forms as seen in chimpanzees and humans when certain social and ecological conditions are fulfilled, but the mobilisation of anciently preserved neurophysiological pathways explains how cooperation is maintained at the group-level and the xenophobic feeling of "us versus they". It is therefore likely that humans share with chimpanzees some commonalities inherited from our last common ancestor, explaining similarities between chimpanzee and human warfare.

Keywords: Intergroup competition, socio-ecology, imbalance of power, collective action problem, parochial cooperation, xenophobia.

INTRODUCTION

Many scholars have debated on the origins of warfare in humans and on its nature, leading to differing views of warfare as an invention (Mead, 2015), as a recently evolved trait in humans (Kelly, 2000), or as an adaptation (Gat, 2008). These debates stem from philosophical discussions rooted in intellectual views of T. Hobbes and J.-J. Rousseau (Otterbein, 1999). For T. Hobbes, war is the natural state of humans, and powerful institutions are necessary to control and buffer "natural" tendencies for selfishness and violence. On the contrary, J.-J. Rousseau, proposed that humans are by nature peaceful and cooperative, and that warfare is an invention of modern states and institutions and their corruptive nature. We will see that it is likely incorrect to oppose, on the one hand, human warfare and selfishness, and, on the other, their peaceful nature and cooperation, given the evolutionary imbrication of intergroup conflicts and cooperation. These debates can be appeased by broader perspectives from ethnography, archaeology, prehistory, anthropology and primatology. These fields propose nuanced views on the origins of collective violence, the conditions favouring the emergence of intergroup conflicts, their adaptive role, and the variability of forms of conflict between groups observed in non-humans, including non-human primates (hereafter "primates").

Evidence for an early origin of warfare in humans, predating agriculture and sedentary societies have recently grown (Kissel and Kim, 2019, Darmangeat, 2020). Shifting away from recent origins of warfare due to resource accumulation in farming societies, the current debate is rather about when such collective forms of violence have emerged across our evolutionary history. Some argue that only high cognitive skills and capacity for symbolism could give rise to warfare (Kissel and Kim, 2019), others that small-scale warfare is part of our evolutionary history, finding its origin in the last common ancestor with bonobos and chimpanzees (Wrangham, 2010). However, scant evidence across archaeological records limits our perspective, and given that behaviour does not fossilize, evolutionary anthropology and primatology can provide a deeper perspective by using extent primates as comparative models. Rather than addressing directly the "when" of the origin of collective violence, analysing patterns of intergroup relationships in primates can shed light on the ultimate and proximate mechanisms enabling intergroup competition to occur and to act as a selective pressure. This, in turn, promotes the analysis of the evolution of adaptations such as territoriality, out-group hostility (xenophobia) and participation to collective actions, essential elements found in human warfare. This helps in understanding the conditions in which escalation of conflicts, leading to extreme forms of intergroup violence, can emerge and constitute evolutionary adaptations.

When using an evolutionary perspective to address questions on the origin of behavioural traits, biologists implicitly posit that such traits have evolved from an ancestral character or form. Natural selection proposes that a trait evolves and is maintained in a population when it confers reproductive success benefits to the individuals presenting this trait. From this evolutionary point of view, warfare is a puzzle, given its cooperative and sacrificial nature, which contradicts predictions from natural selection where individuals should be motivated by their own reproductive interests, especially when their own fitness is reduced to the benefit of the other individuals. The puzzle of cooperation can be considered as solved, thanks to theoretical and empirical advances in animal behaviour and theoretical biology. The main explanations on the evolution of cooperation include by-product mutualism, reciprocity, kin selection and group selection (Dugatkin, 1997). As we will see throughout this paper, mechanisms explaining cooperation with non-kin are at the core of evolutionary explanations of individual participation to intergroup conflicts. Self-sacrifice is an extraordinary form of altruism and finds most of its theoretical explanations in kin selection (Krupp and Maciejewski, 2022), where an individual's self-sacrifice benefits close relatives. While this is a satisfactory explanation in social insects and in small-scale societies mainly composed of related individuals, it does not explain large scale sacrifice as seen in human warfare. Self-sacrifice in primates being rare or almost non-existing, we do not consider it as a defining component of primate intergroup conflicts but rather approach warfare as cooperative and collective actions.

Shall we talk about warfare in primates? Defining warfare is at the core of this edition and is not a simple matter. Human warfare, as compared to other forms of intergroup conflicts observed in animals, can be characterized by a public action resulting in conflicts between groups aiming at asserting domination, resulting in lethal outcomes (Boulestin, 2020). The notion of domination (or dominance) can be applied to intergroup conflicts in primates, and lethal outcomes can happen, even if rare. Conservatively, we use the term intergroup conflicts in a general sense, rather than warfare, even if intergroup conflicts in chimpanzees can be considered as a small-scale, continuous, low intensity state of war. This paper explores empirical and theoretical concepts and mechanisms pertaining to intergroup conflicts in primates, with a specific focus on one of our closest living relatives, chimpanzees (*Pan troglodytes*), to provide an overview of the mechanisms and evolutionary pathways by which intergroup conflict violence intensifies, leading to extreme forms as seen in human small-scale warfare. We first review the mechanistic socio-ecological conditions leading to the intensification of intergroup competition and conflicts, by summarizing the factors explaining the diversity of intergroup relationships observed across primates. This approach reveals that lethal intergroup conflicts are rare in primates, with the remarkable exception of humans and chimpanzees. We then explore the mechanisms and forms of intergroup relationships observed in chimpanzees, to understand the conditions necessary for collective action and lethal violence. We mobilize several key theoretical concepts, such as intergroup dominance (Crofoot and Wrangham, 2010), imbalance of power (Wrangham, 1999), and parochial cooperation (Lemoine et al., 2022). We propose that a key condition for small-scale warfare to occur is to solve collective action problems, which can be achieved by both in-group social cohesion and out-group hostility, formulated by the parochial cooperation model. Small-scale cooperation with non-kin during collective actions, as observed in chimpanzees and humans, is intrinsically linked with out-group hostility. Such traits co-evolved with mechanisms reducing risks of free riding, such as reciprocity and social bonding, enabled by the mobilisation of ancient neurophysiological pathways. Roots of human warfare, as observed in chimpanzees, can be found in a much older evolutionary past than previously thought.

2.VARIABILITY IN TERRITORIALITY AND INTERGROUP RELATIONSHIPS ACROSS PRIMATES

Intergroup conflicts are inherently related to territoriality. In primates, there is considerable variation in forms and intensity of territoriality across taxa, habitats and populations. Territoriality is the expression of intensified intergroup competition (IGC) and can take place at the individual and group levels. Aggressive range defence, primarily driven by ecological incentives and the economic defensibility of an area (Mitani and Rodman, 1979) vary considerably within and between species and populations. This mechanistic and plastic perspective is corroborated by findings of moderately high phylogenetic signal of territoriality across 213 primate species (Kamilar and Cooper, 2013). Ecological pressures can lead to similar social structures in distantly related species, as in spider monkeys and chimpanzees, where both taxa show similar association and territorial patterns (Chapman and Rothman, 2009). Overall, there seem to be relatively poor phylogenetic constraints on the expression of territoriality in primates. However, a recent study found a phylogenetic signal in human interpersonal violence (Gómez et al., 2016), which could relate to the evolutionary link of intergroup conflicts between humans and chimpanzees.

Intergroup relationships in primates span from tolerance, neutrality, avoidance, distant hostile exchanges, to direct confrontations. This variation pertains to the manner in which individuals interact (ranging from affiliative to aggressive), the motivation underlying interacting (such as access to food, mates, territory, or shelter), the spatial and temporal context (including borders, seasonality), and the identity of participants (males, females, individuals of high or low rank; Brown and Crofoot, 2013). Multiple socio-ecological factors explain this variation, including resource distribution and abundance linked to dietary needs of a given species, energetic expenditure trade-offs, population density, history of interactions, group composition and size, dispersal system and individual participation, and collective action problems. We do not provide an exhaustive review of the effects of these factors on each of these facets but rather exemplify the behavioural flexibility of primate species and the socio-ecological conditions and evolutionary pathways leading to an intensification of intergroup conflicts.

2.1 Intergroup competition and resource defence strategies

Territoriality, defined as adaptive behaviours aiming at securing a given area against the intrusion of competitors (neighbours or floaters) occurs when IGC is high at the population scale. IGC for food depends on resource type, on their distribution and on the capacity of species to monopolize them and exclude others from access (Sterck et al., 1997). Therefore, it is high for species relying on sparsely distributed, high quality, monopolizable food, such as fruits. In this case, females whose fitness depends on resources access remain in their natal group to secure food resources, form matrilines with inherited rank, enabling kin-related forms of cooperation. The intensity of IGC can relax within-group relationships among non-kin, with tolerance from high-ranking toward subordinate females, to secure cooperative action during intergroup conflicts. In contrast, for species relying on evenly distributed, non-monopolizable and poor-quality food, such as leaves, IGC is relaxed, females do not form matrilines, female dispersal is not costly and territorial behaviour is lacking. The causal relation between food types, their distribution and the capacity to exclude others from access thus impacts on territoriality and on the extent of range overlap. Depending on site feeding intensity, resource distribution, abundance and patch size, three main forms of resource defence strategies emerge (Brown, 2013), which, in turn, impact on range overlaps and on patterns of territoriality.

1. The core area defence strategy occurs when the core area of a territory contains more important food resources than the periphery, in which case the periphery is not defended, leading to high home-ranges overlaps and high intrusion rates by neighbouring groups. This is observed in white-faced capuchins, where the intensity of intergroup conflict is stronger near core areas, with smaller groups defeating larger groups when intrusions take place closer to the centre of their territory (Crofoot et al., 2008).
2. The boundary defence strategy occurs when more important food resources are located in the periphery, which is defended; in this case, overlap between neighbouring groups is low, territories tend to be exclusive, and periphery territorial behaviour is observed, such as patrolling in wild chimpanzees (Mitani and Watts, 2001).
3. When resources are equally distributed across the territory, a patch resource defence strategy is adopted, and avoidance between neighbouring groups moving between food patches can be observed as in mountain gorillas (Seiler et al., 2017).

These strategies affect rates of interaction with neighbouring groups, history of interactions, and types of interactions (avoidance, approach, exclusion).

2.2 Seasonality and energetic trade-offs

The defense of resources entails variable costs and benefits, depending on the energetic trade-offs made with other activities.

For example, chimpanzee patrolling behaviour incurs energetic costs, since individuals participating increase traveling and decrease feeding and socializing (Amsler, 2009). In addition to distribution and abundance, seasonality in food production affects the ability to defend a territory. In the chimpanzee Kanyawara community from the Kibale National Park, Uganda, seasonality in certain food types increases the chances of intergroup encounters, attracting higher numbers of individuals, but does not explain the escalation of violence (Wilson et al., 2012). In the chimpanzee population of Taï, Ivory Coast, intergroup encounters tend to be more frequent during the dry season, when parties are larger and food availability higher (unpublished data). Higher food availability allows chimpanzees to form larger parties (Doran, 1997) which are more likely to travel further toward the periphery (Wilson et al., 2012; Samuni et al., 2019a). Seasonality in aggressive intergroup encounters is found in multiple primate species: in vervet monkeys, intergroup encounters are more aggressive and violent during times of peak production of valuable and concentrated resources (Harrison, 1983); in blue monkeys, more intolerant intergroup encounters take place when more food is available (Thurau and Cords, 2024). Intergroup encounters in bonobos, although non-aggressive, are also more frequent during times of high food availability (Lucchesi et al., 2020). In some other species and populations seasonality does not seem to influence the nature of intergroup relationships (Verreaux's Sifakas: Koch et al., 2016; Tibetan macaques: Zhao, 1997; Western gorillas: Cooksey et al., 2020). Globally, but this would require further systematic investigation across species and populations, a general trend is that low food availability does not increase intergroup conflicts, but rather the opposite applies: more food allows more energy, longer traveling distances and more resource allocation toward locomotion; also, more available food, especially those of high value, increases the odds of intergroup encounters as they attract more individuals.

2.3 Population density and intergroup dominance

Another factor explaining variation in IGC in primates is population density, directly related to the costs and benefits of defending resources. A comparative study of lethal aggression across the genus *Pan* (Wilson et al., 2014), found that population density determines the escalation of intergroup conflicts, with higher numbers of lethal intergroup aggressions occurring in communities living in higher population density. Similarly, in a population of colobus monkeys, as population grew, more intergroup encounters were witnessed especially when monopolizable food resources were available (Arseneau-Robar et al., 2024). In Japanese macaques, intergroup encounters were more frequent and aggressive in high density populations compared to low-density ones (Sugiura et al., 2002). As population density increases, the per-capita number of available resources decreases, leading to a need for territory expansion and/or increasing needs for territorial defence.

When compared across species of primates, with phylogeny being controlled, group size does not explain the propensity to be aggressive toward neighbours. Instead, variation in frequency of intergroup encounters, across the compared primate species, is mostly explained by differential and unequal distribution of food resources, reflecting the costs and benefits of resource defence (Majolo et al., 2020). However, the same study revealed that across primate species, larger groups are more likely to win encounters against smaller groups (Majolo et al., 2020). In general, smaller groups tend to avoid encounters, especially when outnumbered by opponents, as in gray-cheeked mangabeys (Brown, 2020); or larger groups displace smaller groups as in wedge-capped capuchins (Robinson, 1988), Japanese macaques (Sugiura et al., 2000) and chimpanzees (Lemoine et al., 2020a). Avoiding larger groups seems to be an adaptive strategy minimizing the risks. The mechanistic process of avoidance and displacement as function of relative group size, with larger groups dominating smaller groups, has been operationalized by the intergroup dominance hypothesis (Crofoot and Wrangham, 2010). This model proposes that IGC results in a group hierarchy at the population scale, in which the most dominant groups, who benefit from larger territories, which mediate fitness advantages through access to resources, are more likely to win outgroup contests. Territorial expansions via winning intergroup encounters and displacing neighbours increase feeding opportunities, reduce within-group feeding competition, and therefore offer reproductive benefits. Evidence of intergroup dominance can be found in wedge-capped capuchins, where individuals living in larger groups have a higher reproductive success than those living in smaller groups (Robinson, 1988). In Western chimpanzees, larger groups have larger territories and suffer less neighbour pressure than smaller groups, while reducing neighbour pressure results in shorter interbirth intervals and improved infant survival (Lemoine et al., 2020a and 2020b). In wild baboons, smaller groups displaced by larger groups suffered from short-term avoidance of key resources (Markham and al., 2015), and in Eastern chimpanzees, females living in larger home-ranges have shorter interbirth intervals (Williams et al., 2004) and increased body mass (Pusey et al., 2005). The intergroup dominance hypothesis is an appropriate model linking proximate mechanisms of intergroup interactions (how groups compete) and ultimate explanations of intergroup aggression (why groups compete).

2.4 Group composition, individual participation and collective action problem

Group composition influences individual participation to and thus outcomes of intergroup conflicts. The presence of infants reduces the likelihood of lactating females to participate to intergroup encounters in vervet monkeys (Arseneau-Robar et al., 2017) and in blue monkeys (Cords, 2007). Subordinate female common marmosets participate more to territory defence than reproductive ones (Lazaro-Perea, 2001). These patterns can be explained by the costs of infanticide that can occur during intergroup encounters. However, these patterns are not systematic, as in Verreaux's Sifaka where female participation to intergroup encounters is higher during the lactation period, which is also the period of food scarcity (Lewis et al., 2020). In this case, benefits of securing food resource outweigh the costs of infanticide. In contrast to female participation, male participation can be increased due to the number of infants present in a group: in Eastern chimpanzees, males who have sired more offspring participate more often to border patrols, hereby securing their inclusive fitness (Langergraber et al., 2017). Group composition, especially the number of adult males, impacts on the outcomes of intergroup conflicts. In wild Western chimpanzees, territories are larger in communities that contain more adult males, although the ability to secure a common home-range is guaranteed by efforts from the whole group (Lemoine et al., 2020a). In baboons, the number of adult males predicts the likelihood to win a contest (Markham et al., 2012). In vervet monkeys, the probability to win a contest is determined by the number of participants, especially adult males whose participation is incited by adult females (Arseneau-Robar et al., 2016).

These considerations on the effect of group composition on intergroup conflict leads to the next point of discussion: individual participation. Intergroup conflicts involve action of a certain number of individuals, often unrelated, and present risks of injury or death, as well as opportunity costs. Therefore, individual participation may be limited because of "free-riders", who benefit from the collective action without paying the costs, especially when kin selection inclusive fitness benefits cannot be invoked to promote cooperation and collective action. Collective action problems arise if too many group members fail to participate. Individuals, depending on their specific attributes (sex and rank) may have different incentives to participate (Beehner and Kitchen, 2007). Generally, males tend to engage more in group aggression for mate defence, while females engage for resource defence, as in Verreaux's Sifaka (Lewis et al., 2020). Higher-ranked individuals are more likely to be involved as they have more to gain from resource defence. Reproductive factors matter, since the presence of dependent offspring and access to mates influence aggression, especially among females. In-group dynamics matter, as participation can depend on the behaviour of companions or allies and on the perceived benefits of intimidating rivals or exploring future group transfer opportunities. Interacting with neighbouring groups by the dispersing sex may be used to evaluate opportunities for future transfer or for mating opportunities. Dispersal systems may therefore explain differences in individual participation, where the resident sex has more to gain from territorial defence than dispersing individuals. In fact, the collective action problem is the main argument used to explain why violent and lethal intergroup relationships are rare in primates (Willems and Van Schaik, 2015). A comparative study found that collective action stricto sensu in primates is rarely involved in communal range defence and that territorial behaviour is better interpreted as the outcome of opportunistic and strategic individual-level decisions (Willems et al., 2015). Collective action problems explain why, across primates, home-range overlaps are twice as high in groups with multiple adults of both sexes as compared to groups with only a single adult (Willems et al., 2013). Linear increase of group size leads to collective action problems which may explain why, in some populations, group size is negatively correlated with participation and wining contest, as in Verreaux's Sifaka (Lewis et al., 2020) and in capuchins (Crofoot et al., 2008). In these cases, benefits of resource holding potential (group size) are undermined by collective action problems. After controlling for phylogenetic contrasts, E. P. Willems an C. P. Van Schaik (2015) found that collective action problems can be resolved in species being cooperative breeders (such as banded mongoose; Cant et al., 2002), in those characterized by philopatry of the dominant sex, and in those living in relatively small groups with few members of the dominant sex. We will see below how relevant these findings are regarding out-group conflicts in chimpanzees and humans.

2.5 History of interactions and familiarity

Variation in intergroup encounters, from tolerant to aggressive, is strongly linked to the history of interactions between neighbouring groups. Low rates of interactions mean a low degree of familiarity. Familiarity can also vary at an individual level, where members of the dispersing sex may have a longer interaction history with neighbours than the philopatric sex. The "dear enemy" effect implies less aggressive responses given to familiar versus unfamiliar neighbours, while the "nasty" neighbour effect implies stronger agonistic responses when facing familiar than unfamiliar opponents (Christensen and Radford, 2018). Some primates tend to follow one or the other strategy, like black-and-gold howler monkeys who respond more strongly to strangers than to familiar intruders (Holzmann and Córdoba, 2024). The response to intruders may however vary depending on the habitat and resource distribution, as in Diana monkeys showing nasty neighbour responses in high food availability habitats, but dear enemy responses in low food availability habitats (Decellieres et al., 2021). Wied's black-tuft-ear marmosets live in pairs and show agonistic intergroup interactions in the wild. In captivity, modulation of the familiarity with intruders modified the level of aggression expressed by residents, who were less aggressive toward familiar intruders than to unfamiliar, while the behaviour of intruders did not change with the degree of familiarity with residents (French et al., 1995), A longitudinal study on wild mountain gorillas tested the effect of familiarity on intergroup interactions (Mirville et al., 2018). Interactions were diverse, the majority being non-physically agonistic, while peaceful exchanges and physical aggression were less common. Peaceful interactions mostly involved opponents that contained familiar and related individuals, suggesting that the short dispersal distance of gorillas may facilitate kin-selected intergroup tolerance. Similar mechanisms of familiarity induced by dispersal and kin relations was inferred (Pisor and Surbeck, 2019) in lowland Western gorillas showing high rates of non-aggressive intergroup interactions. Familiarity could also partly explain generally peaceful intergroup relationships in bonobos (Furuichi, 2020). Bonobos are characterized by female dispersal and co-dominance of males and females, and females play a considerable role in reducing within-group aggression (Furuichi, 2011; Moscovice et al., 2019). Kin relatedness with females from neighbouring groups, regular interactions, and female coalitions against male aggression may explain the intergroup general peaceful nature of bonobos. The role of females as the emigrating sex in appeasing intergroup relationships was also emphasized in wild Western chimpanzees (Boesch et al., 2008) with females attempting to interrupt hostile interactions, and observations of affiliative behaviour between males and nulliparous female neighbours. In Eastern chimpanzees, female involvement in intergroup encounters is much less common than in Western chimpanzees, and the majority of intergroup encounters involving females were aggressive, apart from very few cases of peaceful interaction with grooming between members of both sexes (Hashimoto et al., 2020).

2.6 Socio-ecological determinants of the intensification of intergroup conflicts

This brief review of the variability of intergroup relationships and conflicts across primates allows drawing some generic conclusions regarding the socio-ecological conditions leading to an intensification of intergroup conflicts. First, diet and resource distribution determine the intensity of IGC. Intergroup relationships are more hostile and exclusive, leading to territorial behaviour, for species relying on sparse, non-evenly distributed high-quality food resources. Depending on the distribution of resources, variable resource defence strategies can be adopted, leading to varying levels of range overlap and territoriality. Border defence strategy appears to yield more intense territorial behaviour, as in spider monkeys (Aureli et al., 2006) and chimpanzees (Mitani and Watts, 2001). However, the economic defensibility of a given area, determined by the costs and benefits of range defence, can only occur when sufficient resources are available to spend energy in this activity and/or when resource at stake are of important value. Energetic expenditures trade-offs render territorial behaviour season-dependent and energy-dependent. A remarkable pattern is that high food availability tends to increase intergroup conflicts rather than reducing them. Patterns of intergroup dominance arise, with larger and more powerful group dominating smaller ones, with some extreme cases of local extinction of neighbours and expansion of territories (Mitani et al., 2010). Intergroup dominance provides an evolutionary pathway explaining why being territorial. Complexity of individual participation seems to be more tied to individuals' characteristics than to ecological conditions. Males and females may defend a range for different reasons (mate versus resource defence). Motivation for participating to intergroup conflicts depends on individual sex and social status and may be impaired by intersexual conflicts as seen in vervet monkeys where females "punish" males that do not participate to out-group conflicts by reducing their grooming interactions with them (Arseneau-Robar et al., 2016). Individual participation also depends on group composition, such as the number of infants and adult males. Dispersal systems lead to variable history of interactions and incentives to participate but can also reduce the displayed violence and aggressivity, hereby constituting a key for more peaceful intergroup relationships. Variability in individual participation causes however collective action problems and most of primate territorial conflicts seem driven by individual incentives rather than by collective action. This leads to the next part of this essay: when and how can collective action problems be solved, and is this the key for more violent, intense and lethal intergroup conflicts, as seen in humans and chimpanzees?

3. MECHANISMS OF INTERGROUP CONFLICTS IN CHIMPANZEES

3.1 Patterns of chimpanzee territorial behaviour

Chimpanzees live in multi-male multi-female communities composed of related and unrelated individuals, females usually disperse at sexual maturity while males are philopatric (Goodall, 1986; Boesch et Boesch-Achermann, 2000). Social dynamics of chimpanzees are characterized by fission-fusion, where individuals within a community form temporary sub-groupings of variable length and composition. Patterns of fission-fusion vary across populations, in response to ecological conditions, with smaller parties in periods of low food availability (Lehmann et al., 2007). Association patterns between males and females are variable, with some populations characterized by a male-bonded social system, where males home-range encompasses several smaller more or less segregated female core areas. Other populations present a bisexually-bonded social system, where males and females occupy a similar home-range and mixed-sexed parties are more common (Lemoine et al., 2019).

Patterns of territorial behaviour in chimpanzee populations have been extensively described elsewhere (e.g. see Wilson and Wrangham, 2003; Wilson, 2013). First, chimpanzee territorial behaviour is characterized by border defence strategies, with regular border patrols in the periphery of the territory, where individuals travel silently in a coordinated manner, search for signs of neighbours, sniff shrubs and saplings, and stop regularly to listen to the surroundings (Mitani and Watts, 2001 and 2005). Parties undertaking border patrols are more cohesive and larger than non-patrol parties (Samuni et al., 2017). Given their coordinated and cohesive aspect, chimpanzee border patrols constitute a striking example of collective action (Lemoine et al., 2022). Individuals participating to border patrols are mostly males, especially in Eastern chimpanzees (Mitani and Watts, 2005), but adult females and younger individuals can also participate, as in the Western chimpanzees of Taï (Samuni et al., 2017 ; Samuni et al., 2019a). It can be argued that border patrols are low-risk activities and that individuals have little to lose to participate. However, undertaking border patrols is energetically costly, bearing opportunity costs (Amsler, 2009) and can be risky, given the odds to encounter hostile neighbours in overlap areas. However, it is true that risk-minimizing strategies, such as elevation usage to detect neighbours from a distance, can reduce the odds of encountering outnumbering neighbours (Lemoine et al., 2023). Such risk-minimizing strategy may however be an adaptive consequence to the costs inherent to intergroup conflicts. Fitness advantages deriving from border patrols include securing and increasing a feeding territory (Wilson, 2013; Mitani et al., 2010), and protection of current reproductive investment for males (Langergraber et al., 2017). Securing and expanding a territory reduces within-group feeding competition and improves group members fitness. Individual participation to border patrols is explained by self-interested benefits, such as securing current reproductive fitness (infant protection), but also by long-term collective benefits, such as future territory and group size increase (Langergraber et al., 2017).

In chimpanzees, border patrols regularly lead to intergroup encounters. They usually take place in the periphery of the range between neighbouring communities, correspond to distant vocal exchanges, which can escalate into direct encounters with visual and/or physical contact, during which individuals chase and attack the out-group (Goodall, 1986; Boesch and Boesch-Achermann, 2000; Wrangham and Glowacki, 2012). Detecting neighbours triggers signs of excitement, affiliative behaviours but also stress. Intergroup encounters are extremely hostile, stressful (Wittig et al., 2016; Samuni et al., 2019b), with strong signs of xenophobia and can escalate into lethal aggression (Wilson et al., 2014). Attackers in lethal cases are in majority adult males, while victims may also include females, juveniles and infants of both sexes (fig. 1; Wilson et al., 2014). Rates of intergroup killing across chimpanzee populations are comparable with rates in subsistence hunter-gatherer and farmer human populations (Wrangham et al., 2006). Lethal aggression takes the form of coalitionary aggression, facilitated by differences in numbers (Wrangham, 1999), where individuals, both males and females, gang up against a victim at minimum costs. The fission-fusion dynamics of chimpanzees, where parties vary in size and composition, creates the conditions for numerical differences between opponents, which has been operationalized by the imbalance of power hypothesis (Wrangham, 1999). The imbalance of power explains why chimpanzees can kill neighbours when numerical conditions allow for it. Numerical assessment has been demonstrated in chimpanzees in both wild Eastern and Western chimpanzees (Wilson et al., 2001 and 2002; Herbinger et al., 2009), and there is growing evidence that chimpanzees gather pre-emptively information on odds in numbers before approaching or retreating from neighbours at minimum risk (Lemoine et al., 2023). Rates of intergroup killings are variable across populations, with high rates occurring in high population density and for communities containing more adult males (Wilson et al., 2014). However, these factors may not directly impact on rates of killings but rather, in combination with ecological conditions, modify within-group competition and in-group social cohesion, which in turn influence the chance for lethal intergroup conflict. For instance, as compared to some Eastern chimpanzees, Western chimpanzees are more gregarious, due to more predictable food availability and higher predation pressure (Boesch, 1991 and 2019), they display lower rates of fission-fusion and are typically bisexually-bonded (Lemoine et al., 2019). In contrast, in some Eastern chimpanzee populations, females occupy smaller home-ranges and are considered less gregarious than males (Kahlenberg et al., 2008). These between-population differences in social dynamics and grouping patterns lead to a less pronounced imbalance of power in the more gregarious populations and thus reduces the chances to observe lethal outcomes.

These typical territorial behaviours are ubiquitous across chimpanzee populations, as border patrols and violent intergroup encounters, including killings, have been observed in most studied populations (reviewed in Lemoine et al., 2022). Chimpanzee territorial behaviour conveys substantial benefits, mostly centered around securing and increasing a feeding territory. Several hypotheses have been put forward to explain what chimpanzees compete for (Williams et al., 2004), including excluding competitors, protecting offspring and mates, attracting mates and protecting a feeding ground. Even if killing a neighbour directly suppresses competitors, the main outcome of intergroup conflicts is territory expansion, as observed in several populations (Goodall, 1986; Mitani et al. 2010; Nishida et al., 2010). Compatible with the intergroup dominance hypothesis, these territorial expansions demonstrate that chimpanzees mostly compete over a feeding ground. The mate attraction hypothesis has received, so far, less empirical support given that territorial expansion did not systematically lead to an increase of the number of females (Williams et al., 2004), despite few examples of annexation of the territory of females from a neighbouring community, after local extinction of adult males (Nishida et al., 2010; Lemoine et al., 2019).

Territorial behaviour in wild chimpanzees is thus explained by several factors: ultimately, chimpanzees compete for space containing enough resources, and outcomes of winning conflicts provide reproductive success benefits, such as better body condition, faster reproductive rates and higher infant survival. Why then killing neighbours rather than repulsing them, as seen in other primates? The ultimate answer is rather why not killing, given that conditions of a strong imbalance of power can lead to an escalation of violence, up to lethal casualties, at a very low cost for the attackers. Costs of killing are thus reduced by numerical asymmetries. Proximately, how communities of chimpanzees compete can be answered by numerical assessment abilities, by the adoption of pre-emptive behaviour to detect neighbours and minimize risks, by ecological conditions influencing grouping patterns, but importantly by cohesive and coordinated collective actions.

3.2 Collective action, social bonding and parochial cooperation

Chimpanzee territorial behaviour is a striking example of collective action, coupled with a strong sense of "us versus they", as observed in human intergroup conflicts. Chimpanzees regularly cooperate with related and unrelated members of their community, with coordinated prey hunting, polyadic grooming, border patrols and intergroup encounters. In contrast to other primates, collective action during communal range defence seems common in

Fig. 1 – A. Two years old female Western chimpanzee of the North-East group. Victim of an intergroup killing that took place in July 2015 in the Taï National Park she was killed by three adult males from North group, while her mother was trapped by six adult females. Her mother could escape. B. Close-up photo of the same individual, showing a puncture on the forehead (red circle) caused by a bite from one of the attackers.

chimpanzees. How do they solve collective action problems, and what are the mechanisms maintaining social cohesion and cooperation among unrelated individuals, especially in risky situations allowing free-riding?

First, collective action problems can be solved in species where the dominant sex is philopatric and where effective territorial defence is critical for reproductive success and survival (Willems et al., 2013). Male chimpanzees are philopatric and, unlike bonobos they are dominant over females, and effective territorial defence impacts on reproductive success and survival. Higher costs of territorial defence should elicit a stronger collective response by in-group individuals to secure fitness benefits (Samuni et al., 2019b), so in-group cooperation during out-group conflicts is more pronounced. Second, there is now growing evidence, in chimpanzees but also in other primates (Majolo et al., 2016), that social cohesion, especially among unrelated individuals, is reinforced by and during out-group conflicts. Chimpanzee parties are larger in times of intense territoriality, engagement in territorial behaviour predicts reduced in-group male aggression (Samuni et al., 2019b), and in-group cohesion is increased in response to simulated out-group threats (Brooks et al., 2021). Male chimpanzees are more likely to join patrols with males with whom they groomed more (Mitani et Watts, 2001), and males and females participate to intergroup encounters more when adult maternal kin or non-kin social bond partners are present (Samuni et al., 2021). Strong, stable and lasting social relationships seem determinant in successful cooperative territoriality, potentially reducing the risks of defection (Samuni et al., 2021). Chimpanzees build strong social ties among unrelated individuals (Mitani et al., 2000; Langergraber et al., 2009; fig. 2), which enable long-term collective action at the group scale. However, strong social ties must be associated with a stable interaction history between partners, so that individuals can benefit one another over time in a predictable way, especially to support reciprocity. Increased interaction predictability of support between bonded partners can decrease defection during collective actions by synergistically motivating participation and increasing coordination (Samuni et al., 2021). On a proximate level, the oxytocinergic (and arginin-vasopressin) systems play an important role in maintaining social cohesion, but also in promoting out-group hostility as observed in chimpanzees and humans. The oxytocinergic system offers a physiological pathway maintaining group-level cooperation and out-group hostility, perpetuating the feeling of "us versus they".

The articulation of group-level cooperation and out-group hostility has been operationalized with the parochial cooperation model (Lemoine et al., 2022; here fig. 3). In this model, individuals in the in-group are familiar with each other, and social ties, constructed through repeated affiliative interactions and promoted by the oxytocinergic system, constitute a cement by which non-related individuals maintain group-level cooperation. Social ties counter-act collective action problems, leading to better group-level cooperation which, in turn, increases the group competitive ability and winning potential in intergroup conflicts, thereby reducing the negative effects of out-group conflicts on fitness. Strong IGC reinforces in-group favouritism and cohesion, strengthening the cementing power of the social ties, and reinforces out-group hostility through the mobilisation of the oxytocinergic system (Triki et al., 2022). Repeated negative interactions with neighbours may in turn reinforce out-group hostility and xenophobic reactions.

In contrast to chimpanzees, bonobos are less xenophobic and more tolerant during intergroup encounters, showing intergroup affiliative behaviour such as food sharing (Fruth et Hohmann, 2018), although with cross-population variations in hostility (Jaeggi et al., 2016; Fruth and Hohmann, 2018). Reduced IGC in bonobos, likely due to ecological conditions with more abundant and predictable food and female dominance, contrasts with the higher hostility observed in chimpanzees. Given the derived nature of these differences and the more recent process of self-domestication that bonobos underwent (Hare et al., 2012), resulting in reduction of reactive aggression coupled with female co-dominance, it is likely that violent intergroup interactions in Hominins were already present in our last common ancestor (LCA) with both ape species, to the condition that this LCA lived in similar socio-ecological conditions than chimpanzees.

In humans, the parochial altruism hypothesis (Choi and Bowles, 2007) has been proposed to explain the tendency for in-group favouritism and out-group hostility (ethnocentrism), suggesting that out-group conflicts drive in-group cohesion, and that cooperation with non-kin and warfare co-evolved (De Dreu et al., 2014). In this model, groups with more individuals favouring the in-group over the out-group (parochialism) are more cooperative during out-group conflicts. Winning conflicts provides substantial fitness benefits, reinforcing the adaptive value of the parochial cooperative phenotype. The oxytocinergic system could be a potential modulator of human large-scale cooperation (Hurlemann and Marsh, 2017). At some point during human evolution there was a functional expansion of the system, triggering cooperation in response to an outside threat even amongst unfamiliar individuals. Direct reciprocity could be a mechanism enabling long-term affiliative social relationships in small hunter-gatherer societies, where repeated interaction histories between community members play a predictive role in participation to group cooperation (Marlowe and al., 2011; Von Rueden et al., 2019). This suggests that some group level cooperation in humans – if only at a small scale – could be explained following the parochial cooperation model. However, given that the co-evolution of cooperation and warfare is sensitive to population structure (Dyble, 2021) and that expressions of parochial altruism in humans is variable across individuals, groups and situations (Pisor and Ross, 2024), large-scale cooperation in humans (Boyd and Richerson, 1989) requires further explanations mobilising cultural incentives to avoid free-riders, such as punishment, normativity, and prestige.

Fig. 2 – Two Western chimpanzee adult males grooming, with hand clasp,
a typical sign of strong affiliation and social bond among partners.

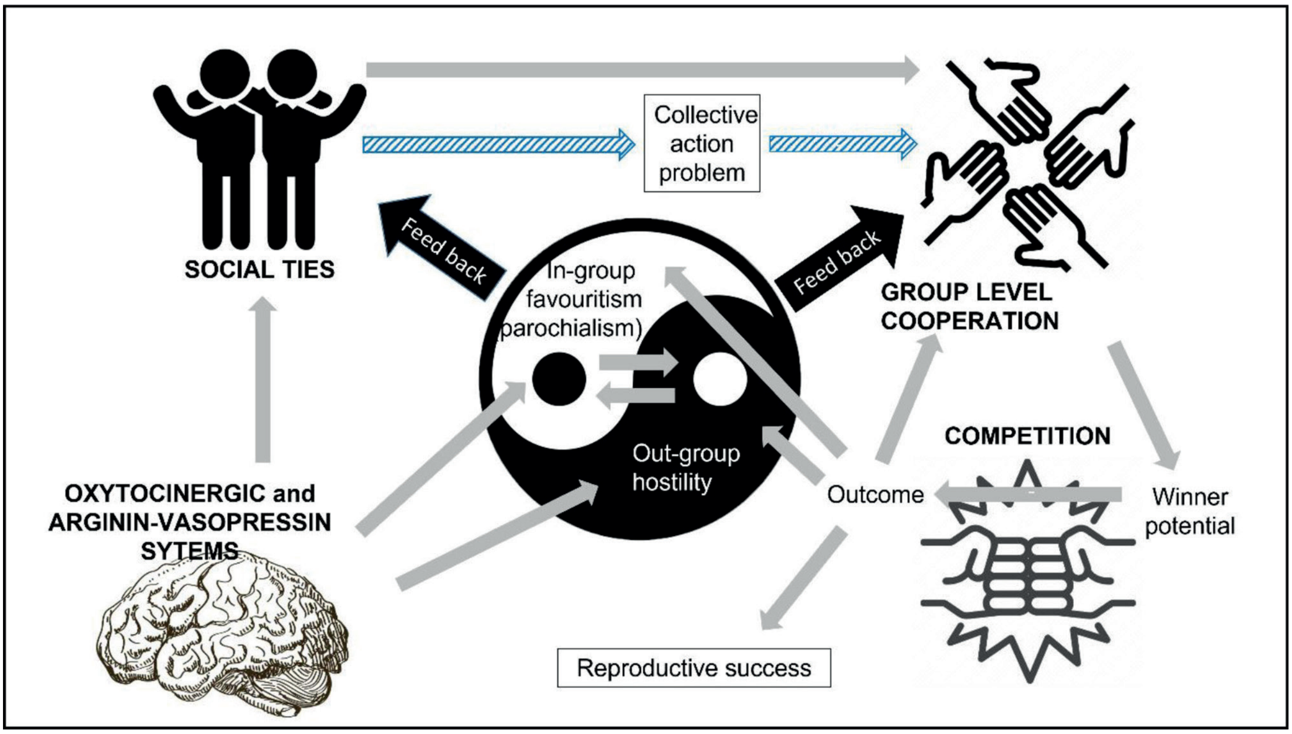

Fig. 3 – Parochial cooperation model (after Lemoine et al., 2022).
The grey arrows represent positive effects, while the shaded blue arrows represent negative effects.

CONCLUSIONS

The purpose of this review was to propose an overview of intergroup conflicts in non-human primates, to extract some generalities on mechanisms and pathways toward an intensification of intergroup conflicts. In brief, intergroup conflicts in primates escalate when resources are worth fighting for, when seasonal and ecological conditions allow for encounters between groups, when asymmetries in power at the group level can occur, and when interactions history reinforces isolation. However, sex dispersal and individual motivations impair participation, leading to collective action problems. Those can be solved by philopatry of the dominant sex and stable and relatively small groups allowing for predictable and lasting social relationships where social ties reinforce group-level cooperation and reduces defection. Substantial fitness benefits yield from territorial expansion, and a strong sense of xenophobia is promoted by physiological pathways and history of interactions. The parochial cooperation model explains how group-level cooperation is reinforced and maintained by intergroup conflicts, promoting xenophobia and a strong in-group feeling with exclusion of strangers, as noted in many aspects of human behaviour. Some physiological responses, preserved across evolutionary times, can be mobilized differently, as in bonobos, so rather than being purely biologically induced, social constructions of the "other" and the "us versus they" are promoted by particular social and environmental conditions.

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DISCUSSION

Arthur Gicqueau: Regarding the video you just showed us, we can see that chimpanzees engage in patrol behavior, where they prepare to attack a rival group. Do we observe the same behavior when they go on hunting other species together, like the colobus?

Sylvain Lemoine: That's a very good question. There is a whole body of theories that link hunting and encounters. Is hunting behavior linked to encounter behavior? In a way, yes. They coordinate, walk in the same direction, and stay quiet. Sometimes it is quite difficult to know whether they are going on a territorial patrol or preparing to hunt. Many hunts also take place when the patrols return. Among chimpanzees, hunting is not mainly about getting food. It is really about strengthening social bonds. They share food, because it is a resource that can be controlled and distributed among those who participated in the hunt. It is also related to territorial behavior, as they need to strengthen social bonds in one way or another. So, there are similarities in behavior. However, when hunting, individuals tend to spread out, while when they go on patrol, they stay really close together, one following the other. In general, these mini-patrols before a hunt are very short, about fifty or a hundred meters. Whereas the patrols you have seen can last for several hours and cover several kilometers.

Marion Corbé: I'm sticking with the hunting theme. I have a question that you answered very quickly at the end, saying that chimpanzees never use weapons in internal conflicts. I remembered a short video of a group of chimpanzees attacking colobus monkeys with sharpened sticks, which the commentary called "spears". Can you tell us a little more about this?

S. L.: They are capable of making tools, including what could be called spears. They sometimes use them when hunting—this is not the case in Tai, it is a different population, and there are cultural differences between the populations. Here, the use of tools during conflicts has never really been observed. Instead they drag branches, they use furniture (not urban, but from the forest!); they drum on trees or twist branches towards rivals, that sort of thing. So these are not exactly weapons. However, the way they make spears is fascinating to observe because there is a sense of foreknowledge and planning. They take a branch of a certain thickness, cut it to a defined length and use the thinner end as the point, holding the thicker end. They also use this technique when they come across a leopard, their main predator. If they have the advantage in numbers, they begin to harass the leopard. The leopard usually takes refuge in a tree where the chimps will grab it by the tail all day long. Sometimes the leopard hides in a hollow tree trunk and chimpanzees have been seen making a spear and trying to insert it into the hollow. It's not exactly the same behavior as when they extract honey, because the branches they use for honey are smaller and they don't hold them in the same way, but the practice of making and using spears is there.

Maurice Fhima: Since yesterday, there has been a lot of talk about cannibalism. Does this behavior exist among apes?

S. L.: Yes, it has been observed but it is not systematic. There is both intragroup and intergroup cannibalism. Intra-group cannibalism is found in very few populations. For example, in Gombe, where J. Goodall worked, competition among females in the same community is quite intense: the availability of food forces them to spread out into areas called "core areas", which are of more or less variable quality. We have therefore seen females kill the young of other females from the same community, and then devoured them—in other words, infanticide followed by cannibalism. There are also some cases of cannibalism after an encounter, after killing a member of a neighboring group. When they hunt together, they eat the whole monkey and leave only the skin. When they kill a baby, they may eat a small piece of it, but this is not at all systematic: it does not occur in all populations, nor after every killing. Another form of cannibalism involves stillborn babies. Stillbirth does sometimes occur and, as with all mammals, energy is an important factor, so the baby is eaten. Moreover, in this case, it is shared. This has been observed in bonobos.

M. F.: Do males ever kill a female's offspring in order to mate with her, as is the case with other animals?

S. L.: That behaviour is typical of gorillas, which have a different social system. Reproduction is monopolized by a single large male, who is certain of his paternity. If he is ousted, one or more new males arrive, who know that they are not the fathers of the young and kill them. This is the evolutionary explanation for infanticide. Infanticide by males within a group is very rare in chimpanzees—if it even happens at all. We only have dubious cases. Between groups, on the other hand, it is attested, and it is often the males who kill. I showed you a photograph of a young chimp that was killed. It's interesting because it happens during the rainy season, when their neighbors, who live in larger communities, are more spread out. The northern group is smaller, so its members can afford to stay together during this season. I got the impression that they took advantage of their numerical superiority. They attacked a female who had a two-year-old infant. All the individuals, males and females, pounced on her and beat her up. She managed to escape, but in the meantime, three males seized the little one and killed it. I have the photographs, you can see the traces of the canines on the brain. But there was no cannibalism afterward.