# The Origins of Human Cooperation Through Intergroup Relations and Their Mechanisms in Our Closest Living Relatives

Corresponding author
Name: Luke Bakic-Pawlak
Affiliation: Akademeia High School
ORCID ID: 0009-0001-9103-7153
Email: lukebakicpawlak@icloud.com
Postal Adress: Al. Waszyngtona 36A, Warsaw, Poland
Phone Number: +48 533 196 596

Co-author
Name: Stuart Wigby
Affiliation: University of Liverpool
ORCID ID: 0000-0002-2260-2948

## Abstract

Cooperation is the foundation of human society, yet our understanding of its evolutionary origins and underlying mechanisms remains limited. This review draws on intergroup encounters in our closest evolutionary relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), to better understand the evolutionary pressures and processes that shaped human cooperation. In chimpanzees, parochialism is demonstrated by in-group bias and coalitionary aggression against rival groups. Chimpanzee parochialism is reinforced by social behaviors within groups, such as fission-fusion dynamics and strong social ties, driven by the fitness benefits – in terms of increased female fecundity– of territorial expansion. By contrast, bonobos cooperate with unrelated strangers from different groups, supported by female coalitions and sociosexual behavior within and between groups, because reduced aggression increases mating opportunities. Physiologically, the oxytocinergic system is crucial in regulating intergroup interactions in chimpanzees, but not in bonobos. Instead, the serotonergic pathway plays an important role in reinforcing bonobos' cooperative tendencies. Human cooperation encompasses extreme forms of both parochialism and cooperation with strangers, raising the question of how we evolved these seemingly contradictory tendencies. The self-domestication hypothesis offers a plausible evolutionary framework, suggesting that selection against reactive aggression has led to increased prosocial and cooperative tendencies. Further research into the cognitive basis of cooperation in bonobos and chimpanzees, as well as genetic comparisons between humans and known domesticated species, can help clarify the roots of our uniquely cooperative nature.

# 1. Introduction

From cells to organisms and individuals to societies, cooperation is a tenet of biology. Across taxa, groups of individuals work together for mutual fitness benefit (Cornwallis, 2018; Hudson & Trillmich, 2008; Sachs et al., 2004). Human cooperation is unmatched in scale (Melis & Semmann, 2010) and drives our success as a species (Bowles, 2006). Social welfare programs, divisions of labor, large-scale conflicts, trade, shared moral standards and political systems all demand group-level cooperation and serve as the basis of our societies. Whether in diplomacy and altruism or warfare and genocide, humans cooperate within groups to achieve their desired aims. Without cooperation, civilization would crumble. To understand human behavior and society, we must understand human cooperation.

However, the adaptive function of cooperation among humans remains unclear (Fehr & Fischbacher, 2003; Apicella & Silk, 2019). If selection favors traits that confer selfish fitness benefits, why do humans go to great lengths to help strangers, or sacrifice themselves for another? Moreover, the mechanisms and evolutionary origins of complex cooperation, especially between unrelated individuals, are yet to be fully understood. This review thus investigates how inter and intragroup cooperation during intergroup encounters in bonobos and chimpanzees can help illuminate the function, origins and mechanisms of human cooperation.

Being our closest evolutionary relatives, with whom we share a recent ancestor roughly 5-7 million years ago (Prüfer et al., 2012), chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) offer a window into our past. They form complex societies and demonstrate cooperative behaviors that mirror some of those observed in humans. For instance, groups of chimpanzees are highly cooperative during intergroup conflicts, displaying lethal aggression and strong in-group cohesion, similar to human warfare (Mitani et al., 2010; Mitani & Watts, 2005; Wrangham & Glowacki, 2012; Lemoine et al., 2023). In contrast, bonobo intergroup encounters often involve tolerance and cooperation towards members of an out-group, otherwise characterized as out-group prosociality, which resembles the human tendency to cooperate with strangers (Tan & Hare, 2013a). By comparing bonobo and chimpanzee cooperation during socially complex intergroup encounters we can understand the selective pressures that enable the evolution of highly cooperative societies. Furthermore, comparisons of the behavioral and endocrinal mechanisms facilitating cooperation in bonobos, chimpanzees and humans can help us understand the processes that make humans so uniquely cooperative.

## 2. Chimpanzees: Warfare and Parochialism

Parochialism, the tendency for in-group bias and out-group hostility, is clearly demonstrated in chimpanzees. When coupled with their high degree of territoriality, parochialism leads to hostile intergroup encounters with neighboring communities (Samuni et al., 2021a). Coalitionary aggression among chimpanzees warrants attention due to the complex sociality and high-level cooperation involved, as well as the implications for understanding the evolution of parochial cooperation in humans.

### 2.1. Coalitionary Attacks and Strategies

#### 2.1.1. Patrols and Warfare

Since they were first observed in the 1970s, coalitionary attacks among chimpanzees have been used to draw parallels with human warfare. Lethally aggressive encounters are prevalent in chimpanzee societies, who compete with neighboring rival groups over territory, females and food (Thompson et al., 2017; Feldblum et al., 2018; Kelly, 2005; Sandel & Watts, 2021; Pusey et al., 2007). Intergroup conflict is followed by territorial expansion into the ranges of defeated neighboring groups (Mitani et al., 2010) and often leads to infanticide (Muller & Mitani, 2005; Lemoine et al., 2022). The consequent expansion of feeding ranges leads to fitness benefits for the attackers such as increased feeding ranges and improved female fecundity [see Section 3.2]. Intense intergroup competition likely acted as a selective pressure that favored parochialism, facilitating the evolution of coalitionary aggression against out-groups despite the potential costs of violent intergroup encounters, such as energy, injury or even death (Gilby et al., 2013; Amsler, 2010).

The extreme coordination and cohesion demonstrated by groups of chimpanzees during intergroup conflicts is such that individuals who are safe from rivals at times rush forwards to defend in-group members attacked by a rival group (Boesch et al., 2008). Encounters with rival groups are usually preceded by collective border patrols (K. E. Langergraber et al., 2017; Mitani & Watts, 2005; D. P. Watts et al., 2006). Predominantly male coalitions patrol territorial boundaries, moving long distances in a single-file line with little socialization or feeding (Mitani et al., 2010; Mitani & Watts, 2005). The extent of female involvement in intergroup encounters varies across populations (Lemoine et al., 2022), but even when participating in patrols, they often act as bystanders during attacks (Muller & Mitani, 2005). Patrolling coalitions slowly and cautiously tread towards border areas, often silent (which is an unusual state for a typically vocal species), highly alert, frequently stopping to sniff the ground for the feces and food remnants of out-group chimpanzees, or listen for signs of rivals (D. Watts & Mitani, 2001; Samuni et al., 2017). Patrollers actively seek vulnerable rival groups and will often lethally attack neighboring groups without provocation (Wrangham & Glowacki, 2012). Yet chimpanzees are not averse to the risks of aggression. The difference in numerical strength of neighboring groups, known as the imbalance of power, determines the decision to attack (Wrangham & Glowacki, 2012). Some mathematical models suggest chimpanzees do not enter conflict unless they outnumber rivals by a factor of at least 1.5 (M. L. Wilson et al., 2002). Patrollers demonstrate a tendency for low-risk attacks where they outnumber their opponents, capitalizing on safe opportunities to attack vulnerable neighbors.

### 2.1.2. The Strategy of Warfare

Since the imbalance of power determines the collective decision for a coalitionary attack, chimpanzees have a number of behavioral adaptations aimed at collecting information on their potential rivals. The subsequent adjustments in decision-making based on the available knowledge serve as risk-reduction tactics for the attackers. For instance, chimpanzees assess the numerical strength of rivals from a distance by listening to their vocalizations in order to decide whether to attack (M. L. Wilson et al., 2002; Herbinger et al., 2009; M. L. Wilson et al., 2001; M. Wilson et al., 2007). Moreover, a study by Lemoine et al. demonstrated that chimpanzees strategically employ topological advantages like high elevation to gather information about rivals (Lemoine et al., 2023). Based on this knowledge, they make low-risk travel decisions, particularly around dangerous areas such as territorial boundaries. Chimpanzees are more likely to rest at high elevations (Lemoine et al., 2023), a behavior that allows for the detection of surrounding rival chimps by hearing, unlike noisier travelling or feeding. Importantly, high-elevation resting is more likely near borders than in central parts of a territory (Lemoine et al., 2023), indicating that the potential presence of rivals impacted resting time and frequency. High elevation tactics serve primarily to detect the distance to rivals rather than their number, which impacts groups' travel decisions. Group travel patterns minimize the likelihood of territorial conflict; for instance, far-away rivals promote the collective decision to advance (Lemoine et al., 2023).

### 2.1.3. Human Applications

Chimpanzees' risk-reducing tactics are remarkable, both in their complexity and their similarity to the strategy of human warfare. In hunter-gatherer and more recent agricultural societies, human warfare has similarly favored low-risk attacks, often using high-elevation or ambushes to strategically reduce risk of injury when attacking a rival group (Wrangham & Glowacki, 2012; Harmon et al., 2004; Titterton, 2022). The employment of these strategies among chimpanzees suggests that high-elevation and risk assessment tactics may have played an important role in intergroup competition from our common ancestor with chimpanzees through human evolution. However, the evolution of coalitionary aggression somewhat differs between humans and chimpanzees, because cultural systems of reward and punishment in humans, such as group-imposed fines and corporal punishment of free-riders, promote greater risk-taking during intergroup conflicts (Mathew & Boyd, 2011; Glowacki & Wrangham, 2013). Human attackers are thus more likely to be injured or killed during intergroup aggression than are chimpanzees in equivalent events (Wrangham & Glowacki, 2012).

The behavioral adaptations of chimpanzees can shed light on the evolution of complex social cognition. Since coordinated decisions to implement risk-reducing tactics require demanding cognitive abilities, it has been hypothesized that warfare drove the evolution of brain size and cognition in humans and chimpanzees (Tooby & Cosmides, 2025; Johnson, 2015). Moreover, chimpanzees demonstrate the importance of intergroup competition in driving in-group cooperation and solidarity. Our understanding of cooperative behaviors and chimpanzee societies could benefit from further research studying the cognitive underpinnings of their capacity for collective decision-making and coalitionary movements, such as the extent to which they understand the intentions or purposes of conspecifics.

## 2.2. Mechanisms of Coalitionary Conflict: Fitness Benefit, Fission-fusion and Social Ties

### 2.2.1. Lethal Coalitionary Aggression Improves Female Fecundity

Although some have suggested that coalitionary aggression might be the result of human encroachment on chimpanzee territories, there is growing evidence that the territorial expansion that follows the defeat of neighboring communities is adaptive (Mitani et al., 2010; M. L. Wilson et al., 2014; Muller & Mitani, 2005). Since group territoriality constrains access to resources, there are fitness benefits associated with dominating neighboring communities to expand territory. In terms of reproductive success, territorial expansion has at least two possible functional explanations. First, home range expansion could lead to the acquisition by males of additional females, thus providing fitness benefits to males by reducing competition for mates and increasing the likelihood that males are reproductively successful. Second, it could improve access to resources, which in turn improves female fecundity, therefore conferring fitness benefits to both males and females. Observational data of males attacking unfamiliar females, especially those with reduced reproductive capacity (Williams et al., 2004), favors the latter explanation. Although increased range size is associated with greater food availability, it does not automatically result in an increased number of females (Williams et al., 2004). Instead, increased food availability confers fitness benefits by increasing female reproductive rates (M. L. Wilson & Wrangham, 2003). Moreover, the theory that coalitionary aggression serves to improve female fecundity, both a male and female fitness benefit, explains female engagement in patrols and intergroup conflicts. If home range expansion served for in-group males to acquire additional females, then coalitionary aggression would only benefit in-group males, failing to account for the participation of in-group females in intergroup conflicts. Therefore, while larger ranges may indirectly attract more females, the immediate consequence of territorial expansion is greater feeding territory and protection from sexual harassment for resident females (Williams et al., 2004). Rather than joining the aggressors' community, females living in shrinking territories will often adjust their ranges to stay within new borders (Williams et al., 2002). The selective benefit of improved female reproductive rates may have favored the evolution of warfare and territorial expansion in humans as well, thereby favoring the evolution of our tendency for parochialism.

Yet chimpanzees' engagement and success in group-level aggression hinges on the possibility of 'cheap victory', which is reliant on social cohesion and cooperation, because these traits reduce the costs of aggression. Therefore, it is crucial to understand the various mechanisms that enable the development of collective action and cooperative behaviors. This is especially true in the case of chimpanzees in this context, where cooperation involves complex sociality and extremely costly aggressive behavior.

#### 2.2.2. Fission-fusion Dynamics and Social Bonds Reinforce In-Group Cohesion

In fission-fusion societies, the size and composition of social groups are fluid, with groups dynamically merging (fusion) or splitting (fission) (Madsen & De Silva, 2024). Fission-fusion enables flexible adjustments to group dynamics depending on ecological factors such as predation, food availability, or increased intergroup competition. When coupled with group territoriality, fission-fusion social structure in chimpanzees (Arcadi, 2018) favors the evolved tendency for lethal coalitionary aggression. During times of increased territoriality, individuals demonstrate reduced modularity (greater cohesion) by associating into larger parties and displaying a lesser tendency to fission (Samuni et al., 2020; Samuni et al., 2017). Fission-fusion contributes to intergroup conflict by enabling the formation of an imbalance of power between rival groups. As explained above, numerical asymmetry significantly reduces risk of harm or injury for aggressors during intergroup conflicts and therefore determines willingness to attack (M. L. Wilson & Wrangham, 2003; Wrangham & Glowacki, 2012). When a community fissions into subgroups (eg. for foraging), they become vulnerable to attacks from larger ranging parties in neighboring groups, such as those on patrol (Lemoine et al., 2022). The capacity to rapidly aggregate large, cohesive patrols in anticipation of conflict gives rise to the imbalance of power necessary for intergroup violence to occur. As a result, fission fusion social structure could exert a selective pressure favoring in-group cohesion and parochialism, because groups with weaker cohesion and increased tendency to fission face greater threat from neighboring ranging parties. Fission-fusion further supports in-group cohesion by enabling chimpanzees to form smaller foraging parties when food is scarce (Riedel et al., 2011), thereby reducing intragroup competition over food and facilitating stronger in-group cohesion. Hunter-gatherer societies, like chimpanzees, form fission-fusion groups (Marlowe, 2005) and seek cheap victories during intergroup conflict (Wrangham & Glowacki, 2012). Therefore, it is likely that fission-fusion played a similar role in creating the conditions for imbalances of power in hunter gatherers, enabling the evolution of human, group level warfare and parochial cooperation.

Moreover, fluid group dynamics facilitate repeated interactions between individuals, forming in-group social ties that are crucial for parochial cooperation and cohesive engagement in coalitions. In chimpanzees, the likelihood of an individual to participate in an intergroup encounter can be predicted by the number of maternal kin and social bond partners present (Samuni et al., 2021b). Ngogo chimpanzees are more likely to patrol together with maternal brothers (K. E. Langergraber et al., 2007) or males they groomed with more (D. Watts & Mitani, 2001). However, kinship has a limited influence on overall cooperation in chimpanzees; most cooperative dyads are non-kin, and paternal brothers do not selectively cooperate (possibly because they cannot reliably recognize each other) (K. E. Langergraber et al., 2007). Nonetheless, any effect of kin presence is predictable given the fitness benefits that can be conferred through kin selection; the same mechanism facilitates coalitionary conflict in eusocial insects like ants (Keller & Chapuisat, 1999). Yet the effect of social bond partners is more notable, as it points to the role played by intragroup sociality and male philopatry in facilitating cooperation. Strong social ties between unrelated individuals are the primary social factor influencing cooperation (Mitani et al., 2000; K. Langergraber et al., 2009a). Similarly, group cooperation in humans often occurs primarily between unrelated individuals (Melis & Semmann, 2010). In chimpanzees, kin and social bond partners, especially male-pair bonds, more frequently support one another in grooming, food sharing or agonistic support (Samuni et al., 2018; Mitani, 2009; K. Langergraber et al., 2009b; Wittig, Crockford, Langergraber, et al., 2014). Social ties create a stable interaction history of increased reciprocal exchange. These social exchanges help mediate within-group competition and establish predictable reciprocity between bond partners, likely reducing the risk of defection during intergroup conflict (Samuni et al., 2021b). Group-level cooperation, involving both kin and non-kin, arises out of a network of social bonds facilitating reciprocity and, in turn, collective action. Yet group territoriality demands cooperation between individuals with varying social relationships, whether they be strong social ties or dyads that barely interact. Since both human and chimpanzee in-group cooperation occurs between unrelated individuals, we may share the same physiology underlying parochial cooperation.

Parochial altruism has defined much of the history of human conflict; war, genocide and racial discrimination often arise out of a hatred for the out-group and a sense of solidarity with the in-group (Choi & Bowles, 2007; Ross & Pisor, 2025). Could understanding the mechanisms of parochialism in chimpanzees may help us navigate these societal ills? It is unlikely that chimpanzee intergroup aggression can be applied as a direct comparison to warfare because the frequency, style and causes of human warfare significantly vary depending on cultural context, often driven by motives not demonstrated in chimpanzees, such as revenge (Wrangham & Glowacki, 2012). Instead, it might be more productive to apply our understanding of chimpanzees to understand the evolutionary origins of parochial cooperation, a social phenomenon that defines intergroup interactions in humans.

# 3. Self-Domestication and Cooperation with Strangers in Bonobos

The human capacity for cooperation with unrelated out-group members has long been considered an evolutionary puzzle (Fehr & Fischbacher, 2003; Nowak & Sigmund, 2005; House et al., 2020) and a uniquely human behavior, often explained in relation to our cultural and linguistical practices (Fehr & Fischbacher, 2003; Apicella & Silk, 2019). Yet are these cooperative behaviors truly unique to humans? Bonobos share some of our cooperative capacities and can provide insights into the evolutionary foundations of human cooperation across social borders.

## 3.1. Observational Evidence

### 3.1.1. Bonobos Cooperate with Unrelated, Out-Group Strangers

Similarly to humans, bonobos demonstrate cooperative tendencies towards unrelated, out-group members with no immediate returns (Samuni & Surbeck, 2023; Tan & Hare, 2013b). Bonobos are especially cooperative towards out-group individuals who also demonstrate high cooperative tendencies (i.e. cooperative assortment). Their social structure facilitates frequent interactions between individuals from different groups (Samuni et al., 2022), thereby enabling the accrual of social knowledge about the cooperative tendencies of out-group individuals. As a result, bonobos can establish relationships of predictable reciprocal exchange across groups, leading to cooperative assortment. However, cooperative behaviors such as food sharing, despite high energetic costs, have a high uncertainty of reciprocation. In a recent study, among the 28 between group, food-sharing dyads observed only 4 exhibited reciprocation (Samuni & Surbeck, 2023). Notably, kin selection (where behaviors are selected due to their reproductive benefit to genetic relatives) is unlikely to play a role in bonobo cooperation, since only 6% of the individuals studied were second-degree relatives or higher (Samuni & Surbeck, 2023). Despite the unpredictability of fitness benefits or reciprocity, out-group food sharing is widely maintained among bonobos.

Intergroup tolerance and cooperation have been further identified in other contexts. Highly social intergroup encounters include instances of out-group members intermingling, playing and sometimes displaying affinitive behaviors such as genital rubbing or copulation (Itani, 1990; Hare et al., 2012). The home ranges of bonobo groups, such as those at Wamba, significantly overlap, leading to temporary group fusions where social units move and forage together for hours or sometimes even days (Furuichi, 2011; Itani, 1990). Even after months or years of separation, distinct social groups demand little more than play and sexual affiliation to reintegrate (Hare et al., 2012). Females play an especially important role as the mediators of intergroup tolerance. Tension during intergroup encounters is eased by female affinitive behaviors with the out-group, which are far less frequent among males. Moreover, females, especially those who have never given birth, often transfer between groups (Itani, 1990). Although males are philopatric, immigration of new females, or even infants, is frequent and generally occurs without incident (Hare et al., 2012; Itani, 1990). Unlike chimpanzees, there are no records of infanticide among bonobos (Furuichi, 2011); in fact, bonobos have been observed to adopt infants from different social groups (Tokuyama et al., 2021). Adoption, play, sexual behavior and out-group prosociality all resemble human behaviors towards strangers from foreign groups (Blumenthal & Young, 2023; De Felice et al., 2023).

### 3.1.2. The Roles of the Sexes

Observations of bonobos at Wamba are crucial in pointing out noteworthy differences in male and female behavior during intergroup interactions. Although it is uncommon, males can selectively cooperate to attack out-group males, while out-group aggression among females is extremely rare; in fact, females sometimes form coalitions with out-group members to attack common targets (Tokuyama et al., 2019). Males compete across groups for mates, yet females are tolerant and cooperative, and their reproductive strategy does not involve intergroup aggression. Given that females are dominant in bonobos due to their ability to form stable coalitions (Surbeck et al., 2025), female superiority offers a means by which bonobos maintain tolerant intergroup relations. Although females are the more cooperative sex, males are still prosocial and establish social bonds with males from different groups. Males do not bias their grooming towards the in-group and often sacrifice time available to affiliate with the in-group to affiliate with out-group individuals, especially other males (Cheng et al., 2022). In humans, the role of females versus males in facilitating cooperation during intergroup contexts is largely unknown. In contrast to bonobos, humans are patriarchal (Zhu & Chang, 2020), suggesting that comparisons of cooperative societies between these species may be limited. Yet it is uncertain whether male dominance is an inherent trait of human society; perhaps, female dominance among bonobos could suggest otherwise – patriarchy is not evolutionarily inevitable. Although cultural norms and sex-based social roles make it difficult to study the inherent nature of male and female roles in human society, further research into female coalition formation in humans' evolutionary past could help us understand whether human societies align with the dominance hierarchy and cooperative behaviors of bonobos.

Although bonobos demonstrate highly prosocial tendencies towards out-groups, it is important to dispel misconceptions that their societies are invariably cooperative and peaceful. Both within and between groups, female coalitions may attack and injure males (Vervafcke et al., 2000; Tokuyama & Furuichi, 2016), and bonobos are at times intolerant of out-groups, even though they tend not to attack them (Hohmann, 2001). Like chimpanzees, bonobos can exhibit group territoriality and intergroup hostility (Moscovice et al., 2022), and they display reduced intragroup aggression during intergroup associations (Tokuyama et al., 2019). These hostile encounters, however, very rarely result in physical aggression (Hare et al., 2012). Thus, while bonobo aggression is less severe than in chimpanzees, bonobos are far from being completely non-aggressive.

The fact that bonobos demonstrate cooperation with strangers, previously considered a notoriously human trait, shows that social norms, complex language systems, marriage unions, kin selection and kin recognition are not required for the evolution of such cooperation. However, the direct parallels to be drawn with humans are limited, because humans exhibit cooperation across social borders on a far larger scale than bonobos, whose out-group cooperation is often dyadic (Samuni & Surbeck, 2023). Nonetheless, bonobos can offer an insight into the evolutionary origins of human out-group cooperation. This review puts forward the self-domestication hypothesis as the most plausible explanation for highly prosocial tendencies in bonobos and suggests that self-domestication provides a viable account of human prosociality.

## 3.2. The Self-Domestication Hypothesis

### 3.2.1. Bonobos: A Case Study for Self-Domestication

The self-domestication hypothesis posits that bonobos have undergone selection against aggression, which has led to the evolution of reduced in-group favoritism and an increase in prosociality towards others, both within and between groups. Behavioral observations of the domestication syndrome in bonobos provide evidence in support of self-domestication. For instance, bonobos share resources with non-selfish interests, helping others even without a request for help or when no desirable social relationship could be formed (Tan & Hare, 2013b; Tan et al., 2017). Moreover, bonobos voluntarily forego their own food in order to interact with strangers (Tan & Hare, 2013b). When unrelated bonobos were given the choice to either monopolize or share food, they preferred to release a recipient bonobo from an adjoining room to share food resources, even though neither kin selection nor conspecific harassment were involved in their decision (Hare & Kwetuenda, 2010). Yet it would be an oversimplification to suggest that selection has enabled out-group cooperation by favoring an overall increase in prosocial tendency. Bonobos' tendency for cooperative assortment (selective cooperation with those likely to reciprocate) suggests that cooperation across social borders is formed by discriminatory social ties, rather than indiscriminatory non-aggression and prosocial tendency. For instance, females do not contribute to intergroup tolerance through unselective cooperation with out-group individuals, but rather through selective social ties within female coalitions.

Yet how did selection favor a reduced propensity for aggression? Given that predation risk does not significantly differ between bonobos and chimpanzees, it was most likely ecological changes in feeding competition that better enabled female cooperation, which allowed the suppression of aggressive males (Hare et al., 2012). Proto-bonobos became isolated from proto-chimpanzees around a million years ago by the Congo river; bonobos are found exclusively to the south of the river, whereas chimpanzees live across West, East and Central Africa (Vigilant, 2007). A higher density of terrestrial food and the absence of gorillas to compete over resources meant that feeding competition among bonobos became relaxed, allowing females to form coalitions (Hare et al., 2012). Despite male-biased sexual dimorphism, stable female coalitions could gain superiority by thwarting aggressive males (Surbeck et al., 2025; Furuichi, 2011; White & Wood, 2007). Moreover, the fitness benefits of male aggression are further reduced by extended female sexual receptivity (Reichert et al., 2002). Due to a longer ovulatory period, males compete less intensely for mating opportunities, thus reducing sexual coercion and the monopolization of mates by domineering males. Increased mating opportunity means that each mating has a lower value, so the benefits of a high rank as a dominant male are reduced. As a result, males display decreased hostility to females in the mating context, and an absence of aggression towards females displaying high fertility (Surbeck & Hohmann, 2013). Since aggression harmed male fitness, male reproductive strategy shifted significantly. Less aggressive males, who avoided the costs of aggression and used kinship ties with their mothers in their natal communities to access females, received greater fitness benefits (Furuichi, 2011; Surbeck et al., 2011). Male aggression was rendered ineffective, and reduced aggression became a selective advantage. Consequently, males evolved phenotypes consistent with domestication.

As reviewed by Hare et al., the phenotypic differences between bonobos and chimpanzee are analogous to the differences between domesticated species and their close, non-domesticated relatives (Hare et al., 2012). For instance, bonobos frequently engage in intensive play (Palagi, 2006; Palagi & Paoli, 2007) or sexual behavior, the majority of which occurs between same-sex partners and is thus non-conceptive (Moscovice et al., 2019; Moscovice et al., 2017). Compared to chimpanzees, bonobos have more gray matter in areas of the brain responsible for perceiving distress and a larger neural pathway involved in control of aggressive impulses as well as biases against harming others (Rilling et al., 2012). By supporting empathy in bonobos, these neural pathways enable the prevalence of sex and play in bonobos, therefore supporting their prosocial behaviors. Morphological traits such as reduced cranial size, reduced facial projection, reduced tooth and mandible size and delayed skull development are shared between bonobos and domesticates, further indicating the likelihood of self-domestication.

### 3.2.2. Self-domestication in Humans

Is self-domestication a plausible account of human evolution? Compared to around 200,000 years ago, contemporary humans have shorter faces, a 40% reduction in brow ridge projection in the skull and reduced sexual dimorphism, changes consistent with those found in domesticated animal species (Meijer, 2024). Moreover, humans share many of bonobos' behavioral traits, such as the propensity to play, share food or behave altruistically to strangers (Bowles, 2006; Tan & Hare, 2013b; De Felice et al., 2023; Blumenthal & Young, 2023). The extreme altricial nature of humans, expanded developmental period, and cognitive abilities for cooperative communication, are further indications of the domestication syndrome in humans (Hare, 2017). Further research into the parallels between humans and domesticates is needed to definitively establish whether self-domestication offers a viable explanation of human cooperation.

If humans have undergone self-domestication, there is no indication that it emerged from strong female coalitions thwarting aggressive males, as it did in bonobos. Instead, human domestication most likely occurred through collective male conspiracies capable of subduing other domineering, bullying males, who used aggressive force to their advantage. As suggested by Wrangham, language-based conspiracy between lower-rank males enabled them to collectively expel, kill or subdue aggressive dominant males (Wrangham, 2019). Consequently, a high rank in the human male hierarchy stems from negotiation ability and alliance formation, rather than brute force. Yet it seems contradictory to suggest that reduced aggression emerged from collective action against aggressively dominant individuals, when collective acts of killing or expelling another individual are, by definition, aggressive. Moreover, human self-domestication seems difficult to reconcile with our propensity for war and mass violence. Here, it is important to distinguish between proactive (premeditated) aggression, such as warfare or execution, and reactive (impulsive) aggression, often displayed in unplanned fights over food or mates. These different types of aggression have separate neurobiological underpinnings and cannot be equated (Wrangham, 2018). The distinction is important, because selection has likely influenced these types of aggression independently. Fitness benefits gained by attackers during intergroup warfare or within-group executions do not have to undermine selection against reactive aggression. Through language and complex cognition, domineering males exhibiting reactive aggression were thwarted, making reactive aggression maladaptive. The long-term effect of killing, expelling and intimidating dominating individuals with a high tendency for reactive aggression is a reduction in reactive aggression. The question of whether humans are inherently aggressive is thus answered:

although we have a high tendency for proactive aggression, our inclination for reactive aggression is low.

Studying cooperation in bonobos offers insights into the evolution of human cooperation and suggests the possibility that self-domestication could be prevalent in highly cooperative species. Further research into the genetic basis of the domestication syndrome in bonobos and other domesticates could be an avenue to identify genetic similarities in humans and other mammals, helping us determine the prevalence of self-domestication as an evolutionary pathway.

## 3.3 Socio-sexuality: The Medium of Out-Group Cooperation

Although self-domestication potentially explains the evolutionary pathway that favored reduced aggression in the long-term, it provides limited insight into the social mechanisms that maintain cross-border cooperation. Evidence suggests that sexual relations are a crucial social mech in facilitating cooperation. Sexual interactions among bonobos likely act to reduce social tension. Bonobos, as well as chimpanzees, have been shown to use genital contact in contexts of elevated social tension to prevent the escalation of conflict and diffuse tension (Brooker et al., 2025). Both species use affiliative contact more generally as a means of offering reassurance to others, such as towards a distressed victim after a fight or prior to feeding (in the context of potential competition) (Brooker et al., 2025). These means of reducing social tension are especially pronounced among bonobos. The majority of bonobo sociosexual behaviors do not serve a reproductive function (Moscovice et al., 2019), and likely help facilitate their cooperative behaviors (Moscovice et al., 2017; Brooker et al., 2025). The frequency of sexual interactions between female and opposite sex pairs positively predicts the frequency of non-kin coalitionary support (Moscovice et al., 2019). Therefore, cooperation with strangers, outside of kinship and pair-bonds, is strongly facilitated by the proliferation of same-sex affiliative behaviors. In some cases, socio-sexual behavior plays a similar role in humans. In Ancient Sparta, for instance, pairs of Spartan soldiers were matched as each other's' concubines, in order to improve social cohesion and reduce within-group hostility in the army (Bertosa, 2009).

# 4. The Role of Endocrinal Pathways as Proximate Mechanisms of Cooperation

Since behavior is determined by neuroendocrine regulation, understanding cooperation within and between groups demands an understanding of its endocrinal pathways. Insights into the mechanisms of cooperation in our closest living relatives can help clarify the roots of cooperation in our evolutionary ancestors. Moreover, comparing proximate mechanisms of human cooperation to those of chimpanzees and bonobos could underpin an explanation for the uniqueness of human cooperation.

## 4.1. The Oxytocinergic System Modulates Parochialism in Chimpanzees

The oxytocinergic system, a neural pathway responsible for releasing oxytocin, is crucial in reinforcing parochial cooperation in the context of intergroup conflict. In chimpanzees, oxytocin is linked to prosocial behavior towards both kin and non-kin group members, such as grooming (Crockford et al., 2013) or food sharing (Wittig, Crockford, Deschner, et al., 2014). Oxytocin more broadly modulates social memory, in-group cohesion and cooperation (Donaldson & Young, 2008; Insel, 2010; Arueti et al., 2013). Consequently, both before and after intergroup conflicts, where chimpanzees demonstrate extreme parochial cooperation and cohesion, they experience increased urinary oxytocin content (Samuni et al., 2017). Similarly, higher oxytocin levels were present before border patrol initiation (Samuni et al., 2017). Oxytocin reduces defection and strengthens in-group bias during coalitionary attacks, therefore enabling the cohesive behaviors displayed during intergroup encounters. Since the oxytocinergic system also underpins cohesion and parochial altruism in intergroup conflict in humans (De Dreu et al., 2010), it likely served to regulate parochialism in our common ancestor. In both humans and chimpanzees, the perception of an external, out-group threat draws individuals together into a cohesive unit, hostile to the out-group.

## 4.2. Endocrinal Pathways of Out-Group Cooperation in Bonobos

The serotonergic system plays a significant role in bonobo social tolerance. Compared to chimpanzees, bonobos have twice the density of serotonergic axons in the amygdala

(Stimpson et al., 2016), a region of the brain that regulates emotional responses and social decision-making (Šimić et al., 2021). Variation in serotonergic innervation affects reactivity to the social environment. Higher serotonin levels lead to decreased neuronal excitability in response to emotionally arousing contexts, including by dampening the 'fight or flight' response (Wolf et al., 2018; Stimpson et al., 2016). Serotonin's suppression of hyper-reactivity in the amygdala helps enable peaceful intergroup interactions in bonobos by increasing impulse control and inhibiting reactive aggression. Similarly, higher serotonin levels in humans promote social interaction, decreased aggression and impulse control (Young & Leyton, 2002; Colwell et al., 2024; Kiser et al., 2012). Given its role in facilitating prosociality, a developed serotonergic pathway is likely a key characteristic of self-domestication.

Peaceful intergroup interactions are further reinforced by testosterone activity during competition. In a controlled experimental setting, bonobos exhibited blunted testosterone responses in contexts of dyadic feeding competition, consistent with self-domestication and reduced male-male competition (Wobber et al., 2010). These findings are corroborated by observations of wild bonobos, where male testosterone levels did not rise during intergroup encounters, even when encounters were hostile (Cheng et al., 2022). Lower testosterone activity could contribute to reduced territoriality and improved out-group tolerance in male bonobos, thus aiding the formation of intergroup male-male pair bonds.

## 4.3. The Endocrinal Basis for Variations in Intergroup Relations Between Chimpanzees and Bonobos

Unexpectedly, oxytocin activity in bonobos, unlike in humans, does not increase in the presence of out groups nor does it regulate prosociality and intergroup tolerance (Cheng et al., 2025). Given the low threat posed by neighboring groups in bonobos, the presence of out-groups does not necessitate the increased in-group cohesion and oxytocin activation demonstrated in chimpanzees. In bonobos, oxytocin stimulation is limited to within-group contexts such as grooming (Brooks et al., 2022) or female homosexual interactions, used to demonstrate social tolerance (Moscovice et al., 2019). The negligible influence of oxytocin activity during intergroup interactions in bonobos indicates a molecular basis for their behavioral differences with chimpanzees and highlights the role of oxytocin activity in reinforcing parochialism. Since the oxytocinergic system has been highly conserved throughout evolution (Yamashita & Kitano, 2013), it likely played a crucial role in the evolution of parochial cooperation and warfare in humans.

Variations in the vasopressin receptor gene, which strongly influence sociability (Walum et al., 2012; Ahern et al., 2021; Barrett et al., 2013), offer a genetic explanation for the behavioral differences between chimpanzees and bonobos. Unlike chimpanzees, all individuals in large bonobo sampling populations have retained the DupB region of the vasopressin receptor gene. The deletion of DupB is specific to chimpanzees and occurred after the sister-species diverged from one another (Staes et al., 2014). DupB contains a microsatellite known as RS3, which is linked to variation in social behavior (Yirmiya et al., 2006; Nishina et al., 2019), and DupB's deletion is associated with a reduction in sociability (Mulholland et al., 2020). While DupB deletion is not universal in chimpanzees, and behavioral traits such as cooperation are polygenic, the markedly lower frequency of the DupB region and RS3 microsatellite in chimpanzee populations points to a genetic basis for their aggressive tendencies (Staes et al., 2014). Similar genetic variations may determine human aggression and prosociality. Further research into these variations in humans, as compared to bonobos and chimpanzees, could therefore help reveal the genetic basis of human social cooperation and aggression.

# 5. Conclusions

Our closest evolutionary relatives provide a window into the nature, origins and mechanisms of human cooperation. Bonobos and chimpanzees each offer a perspective into one of the two seemingly contradictory behavioral tendencies that determine human intergroup relations: parochial aggression and cooperation with strangers.

Parochialism in chimpanzees, where cooperation is based on in-group bias and out-group hostility, enables group territoriality and coalitionary aggression. Violent intergroup conflict in chimpanzees leads to territorial expansion, which increases female fecundity; this adaptive benefit likely led to the proliferation of warfare in hunter gatherers. Fission-fusion social structure, strong social bonds and the oxytocinergic system are among the key processes enabling in-group solidarity and collective action under threat. Several behaviors and underlying mechanisms of parochialism are shared between humans and chimpanzees, and were therefore likely present in our last common ancestor.

In contrast, bonobos display remarkable tolerance and prosociality towards strangers and out-groups, where stable female coalitions mediate cooperation. Bonobos rely on affiliative behaviors, sexual interactions as well as serotonin and testosterone, not oxytocin, to mitigate aggressive competition both within and between groups. Their phenotypes are consistent with the self-domestication hypothesis, in which selection against aggression enabled the evolved tendency for out-group cooperation. Self-domestication offers a plausible explanation of human cooperation. Human self-domestication likely occurred by selection against reactive aggression, facilitated by our cognitive abilities for complex language and cultural institutions. However, further research is needed to affirm the self-domestication hypothesis in humans, including genomic and neurobiological comparisons with known domesticates.

Although cognition is notoriously difficult to study, our understanding of bonobo and chimpanzee cooperation could significantly benefit from a greater consideration of their cognitive capabilities. Many of their cooperative behaviors require complex cognition, such as an understanding of the motives of others, or the ability to communicate intentions and make strategic decisions. If we could advance our knowledge of the neurobiological basis of cognition in chimpanzees and bonobos, we could identify relevant areas of research for an improved understanding of human neurobiology and social cognition. Such research would be applicable to our navigation of social interactions, including our capacity for theory of mind (the ability to ascribe mental states to others).

Moreover, our knowledge of how chimpanzees and bonobos resolve conflicts of interest is incomplete. When individuals cooperate, particularly in the complex and costly manner of bonobos and chimpanzees, they must overcome their competing interests, demanding that individuals provisionally temper their competitive urges. Additional research on competing interests in these species, including through controlled experimental studies, could have implications for understanding human methods of resolving disputes. Settling conflicts of interests is crucial at all organizational levels of human society, whether it be international diplomacy or individual disputes. By examining human cooperation through the lens of intergroup encounters in our closest evolutionary relatives, we stand to better understand our societies, our interactions, and the broader animal kingdom.

# Bibliography

Ahern, T. H., Olsen, S., Tudino, R., & Beery, A. K. (2021). Natural variation in the oxytocin receptor gene and rearing interact to influence reproductive and nonreproductive social behavior and receptor binding. *Psychoneuroendocrinology*, *128*, 105209. https://doi.org/10.1016/j.psyneuen.2021.105209

Amsler, S. J. (2010). Energetic costs of territorial boundary patrols by wild chimpanzees. *American Journal of Primatology*, *72*(2), 93–103. https://doi.org/10.1002/ajp.20757

Apicella, C. L., & Silk, J. B. (2019). The evolution of human cooperation. *Current Biology*, *29*(11), R447–R450. https://doi.org/10.1016/j.cub.2019.03.036

Arcadi, A. C. (2018). *Wild Chimpanzees: Social Behavior of an Endangered Species* (1st ed.). Cambridge University Press. https://doi.org/10.1017/9781108178303

Arueti, M., Perach-Barzilay, N., Tsoory, M. M., Berger, B., Getter, N., & Shamay-Tsoory, S. G. (2013). When Two Become One: The Role of Oxytocin in Interpersonal Coordination and Cooperation. *Journal of Cognitive Neuroscience*, *25*(9), 1418–1427. https://doi.org/10.1162/jocn_a_00400

Barrett, C. E., Keebaugh, A. C., Ahern, T. H., Bass, C. E., Terwilliger, E. F., & Young, L. J. (2013). Variation in vasopressin receptor (Avpr1a) expression creates diversity in behaviors related to monogamy in prairie voles. *Hormones and Behavior*, *63*(3), 518–526. https://doi.org/10.1016/j.yhbeh.2013.01.005

Bertosa, B. (2009). Sacrifice to Eros and Homosexuality in the Spartan Army. *War & Society*, *28*(2), 1–19. https://doi.org/10.1179/072924709793054624

Blumenthal, S. A., & Young, L. J. (2023). The Neurobiology of Love and Pair Bonding from Human and Animal Perspectives. *Biology*, *12*(6), 844. https://doi.org/10.3390/biology12060844

Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup conflicts among chimpanzees in Taï National Park: Lethal violence and the female perspective. *American Journal of Primatology*, *70*(6), 519–532. https://doi.org/10.1002/ajp.20524

Bowles, S. (2006). Group Competition, Reproductive Leveling, and the Evolution of Human Altruism. *Science*, *314*(5805), 1569–1572. https://doi.org/10.1126/science.1134829

Brooker, J. S., Webb, C. E., Van Leeuwen, E. J. C., Kordon, S., De Waal, F. B. M., & Clay, Z. (2025). Bonobos and chimpanzees overlap in sexual behaviour patterns during social tension. *Royal Society Open Science*, *12*(3), 242031. https://doi.org/10.1098/rsos.242031

Brooks, J., Kano, F., Yeow, H., Morimura, N., & Yamamoto, S. (2022). Testing the effect of oxytocin on social grooming in bonobos. *American Journal of Primatology*, *84*(12), e23444. https://doi.org/10.1002/ajp.23444

Cheng, L., Samuni, L., Deschner, T., & Surbeck, M. (2025). Oxytocin activity is not linked to out-group prosociality in wild bonobos. *Scientific Reports*, *15*(1), 19408. https://doi.org/10.1038/s41598-025-00209-w

Cheng, L., Samuni, L., Lucchesi, S., Deschner, T., & Surbeck, M. (2022). Love thy neighbour: Behavioural and endocrine correlates of male strategies during intergroup encounters in bonobos. *Animal Behaviour*, *187*, 319–330. https://doi.org/10.1016/j.anbehav.2022.02.014

Choi, J.-K., & Bowles, S. (2007). The Coevolution of Parochial Altruism and War. *Science*, *318*(5850), 636–640. https://doi.org/10.1126/science.1144237

Colwell, M. J., Tagomori, H., Shang, F., Cheng, H. I., Wigg, C. E., Browning, M., Cowen, P. J., Murphy, S. E., & Harmer, C. J. (2024). Direct serotonin release in humans shapes aversive learning and inhibition. *Nature Communications*, *15*(1), 6617. https://doi.org/10.1038/s41467-024-50394-x

Cornwallis, C. K. (2018). Cooperative breeding and the evolutionary coexistence of helper and nonhelper strategies. *Proceedings of the National Academy of Sciences*, *115*(8), 1684–1686. https://doi.org/10.1073/pnas.1722395115

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1755), 20122765. https://doi.org/10.1098/rspb.2012.2765

De Dreu, C. K. W., Greer, L. L., Handgraaf, M. J. J., Shalvi, S., Van Kleef, G. A., Baas, M., Ten Velden, F. S., Van Dijk, E., & Feith, S. W. W. (2010). The Neuropeptide Oxytocin Regulates Parochial Altruism in Intergroup Conflict Among Humans. *Science*, *328*(5984), 1408–1411. https://doi.org/10.1126/science.1189047

De Felice, S., Hamilton, A. F. D. C., Ponari, M., & Vigliocco, G. (2023). Learning *from* others is good, *with* others is better: The role of social interaction in human acquisition of new knowledge. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1870), 20210357. https://doi.org/10.1098/rstb.2021.0357

Donaldson, Z. R., & Young, L. J. (2008). Oxytocin, Vasopressin, and the Neurogenetics of Sociality. *Science*, *322*(5903), 900–904. https://doi.org/10.1126/science.1158668

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, *425*(6960), 785–791. https://doi.org/10.1038/nature02043

Feldblum, J. T., Manfredi, S., Gilby, I. C., & Pusey, A. E. (2018). The timing and causes of a unique chimpanzee community fission preceding Gombe's "Four-Year War." *American Journal of Physical Anthropology*, *166*(3), 730–744. https://doi.org/10.1002/ajpa.23462

Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology: Issues, News, and Reviews*, *20*(4), 131–142. https://doi.org/10.1002/evan.20308

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373–381. https://doi.org/10.1007/s00265-012-1457-6

Glowacki, L., & Wrangham, R. W. (2013). The Role of Rewards in Motivating Participation in Simple Warfare. *Human Nature*, *24*(4), 444–460. https://doi.org/10.1007/s12110-013-9178-8

Hare, B. (2017). Survival of the Friendliest: *Homo sapiens* Evolved via Selection for Prosociality. *Annual Review of Psychology*, *68*(1), 155–186. https://doi.org/10.1146/annurev-psych-010416-044201

Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*, *20*(5), R230–R231. https://doi.org/10.1016/j.cub.2009.12.038

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573–585. https://doi.org/10.1016/j.anbehav.2011.12.007

Harmon, R. S., Dillon, F. H., & Garver, J. B. (2004). Perspectives on Military Geography: The Military Operating Environment. In D. R. Caldwell, J. Ehlen, & R. S. Harmon (Eds.), *Studies in Military Geography and Geology* (pp. 7–20). Springer Netherlands. https://doi.org/10.1007/978-1-4020-3105-2_2

Herbinger, I., Papworth, S., Boesch, C., & Zuberbühler, K. (2009). Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: A playback study. *Animal Behaviour*, *78*(6), 1389–1396. https://doi.org/10.1016/j.anbehav.2009.09.010

Hohmann, G. (2001). Association and social interactions between strangers and residents in bonobos (Pan paniscus). *Primates*, *42*(1), 91–99. https://doi.org/10.1007/BF02640692

House, B. R., Kanngiesser, P., Barrett, H. C., Yilmaz, S., Smith, A. M., Sebastian-Enesco, C., Erut, A., & Silk, J. B. (2020). Social norms and cultural diversity in the development of third-party punishment. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1925), 20192794. https://doi.org/10.1098/rspb.2019.2794

Hudson, R., & Trillmich, F. (2008). Sibling competition and cooperation in mammals: Challenges, developments and prospects. *Behavioral Ecology and Sociobiology*, *62*(3), 299–307. https://doi.org/10.1007/s00265-007-0417-z

Insel, T. R. (2010). The Challenge of Translation in Social Neuroscience: A Review of Oxytocin, Vasopressin, and Affiliative Behavior. *Neuron*, *65*(6), 768–779. https://doi.org/10.1016/j.neuron.2010.03.005

Itani, G. (1990). *Relations between Unit-Groups of Bonobos at Wamba, Zaire: Encounters and Temporary Fusions* (No. 3). The Center for African Area Studies, Kyoto University. https://doi.org/10.14989/68066

Johnson, D. D. P. (2015). Leadership in War: Evolution, Cognition, and the Military Intelligence Hypothesis. In D. M. Buss (Ed.), *The Handbook of Evolutionary Psychology* (1st ed., pp. 1–23). Wiley. https://doi.org/10.1002/9781119125563.evpsych229

Keller, L., & Chapuisat, M. (1999). Cooperation among Selfish Individuals in Insect Societies. *BioScience*, *49*(11), 899–909. https://doi.org/10.2307/1313649

Kelly, R. C. (2005). The evolution of lethal intergroup violence. *Proceedings of the National Academy of Sciences*, *102*(43), 15294–15298. https://doi.org/10.1073/pnas.0505955102

Kiser, D., SteemerS, B., Branchi, I., & Homberg, J. R. (2012). The reciprocal interaction between serotonin and social behaviour. *Neuroscience & Biobehavioral Reviews*, *36*(2), 786–798. https://doi.org/10.1016/j.neubiorev.2011.12.009

Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences*, *104*(19), 7786–7790. https://doi.org/10.1073/pnas.0611449104

Langergraber, K. E., Watts, D. P., Vigilant, L., & Mitani, J. C. (2017). Group augmentation, collective action, and territorial boundary patrols by male chimpanzees. *Proceedings of the National Academy of Sciences*, *114*(28), 7337–7342. https://doi.org/10.1073/pnas.1701582114

Langergraber, K., Mitani, J., & Vigilant, L. (2009a). Kinship and social bonds in female chimpanzees ( *Pan troglodytes* ). *American Journal of Primatology*, *71*(10), 840–851. https://doi.org/10.1002/ajp.20711

Langergraber, K., Mitani, J., & Vigilant, L. (2009b). Kinship and social bonds in female chimpanzees ( *Pan troglodytes* ). *American Journal of Primatology*, *71*(10), 840–851. https://doi.org/10.1002/ajp.20711

Lemoine, S. R. T., Samuni, L., Crockford, C., & Wittig, R. M. (2022). Parochial cooperation in wild chimpanzees: A model to explain the evolution of parochial altruism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1851), 20210149. https://doi.org/10.1098/rstb.2021.0149

Lemoine, S. R. T., Samuni, L., Crockford, C., & Wittig, R. M. (2023). Chimpanzees make tactical use of high elevation in territorial contexts. *PLOS Biology*, *21*(11), e3002350. https://doi.org/10.1371/journal.pbio.3002350

Madsen, A., & De Silva, S. (2024). Societies with fission–fusion dynamics as complex adaptive systems: The importance of scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *379*(1909), 20230175. https://doi.org/10.1098/rstb.2023.0175

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(2), 54–67. https://doi.org/10.1002/evan.20046

Mathew, S., & Boyd, R. (2011). Punishment sustains large-scale cooperation in prestate warfare. *Proceedings of the National Academy of Sciences*, *108*(28), 11375–11380. https://doi.org/10.1073/pnas.1105604108

Meijer, H. (2024). Janus faced: The co-evolution of war and peace in the human species. *Evolutionary Anthropology: Issues, News, and Reviews*, *33*(3), e22027. https://doi.org/10.1002/evan.22027

Melis, A. P., & Semmann, D. (2010). How is human cooperation different? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1553), 2663–2674. https://doi.org/10.1098/rstb.2010.0157

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, *59*(4), 885–893. https://doi.org/10.1006/anbe.1999.1389

Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, *70*(5), 1079–1086. https://doi.org/10.1016/j.anbehav.2005.02.012

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507–R508. https://doi.org/10.1016/j.cub.2010.04.021

Moscovice, L. R., Douglas, P. H., Martinez-Iñigo, L., Surbeck, M., Vigilant, L., & Hohmann, G. (2017). Stable and fluctuating social preferences and implications for cooperation among female bonobos at L ui K otale, S alonga N ational P ark, DRC. *American Journal of Physical Anthropology*, *163*(1), 158–172. https://doi.org/10.1002/ajpa.23197

Moscovice, L. R., Hohmann, G., Trumble, B. C., Fruth, B., & Jaeggi, A. V. (2022). Dominance or Tolerance? Causes and consequences of a period of increased intercommunity encounters among bonobos (Pan paniscus) at LuiKotale. *International Journal of Primatology*, *43*(3), 434–459. https://doi.org/10.1007/s10764-022-00286-y

Moscovice, L. R., Surbeck, M., Fruth, B., Hohmann, G., Jaeggi, A. V., & Deschner, T. (2019). The cooperative sex: Sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions. *Hormones and Behavior*, *116*, 104581. https://doi.org/10.1016/j.yhbeh.2019.104581

Mulholland, M. M., Navabpour, S. V., Mareno, M. C., Schapiro, S. J., Young, L. J., & Hopkins, W. D. (2020). *AVPR1A* variation is linked to gray matter covariation in the social brain network of chimpanzees. *Genes, Brain and Behavior*, *19*(4), e12631. https://doi.org/10.1111/gbb.12631

Muller, M. N., & Mitani, J. C. (2005). Conflict and Cooperation in Wild Chimpanzees. In *Advances in the Study of Behavior* (Vol. 35, pp. 275–331). Elsevier. https://doi.org/10.1016/S0065-3454(05)35007-8

Nishina, K., Takagishi, H., Takahashi, H., Sakagami, M., & Inoue-Murayama, M. (2019). Association of Polymorphism of Arginine-Vasopressin Receptor 1A (AVPR1a) Gene With Trust and Reciprocity. *Frontiers in Human Neuroscience*, *13*, 230. https://doi.org/10.3389/fnhum.2019.00230

Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, *437*(7063), 1291–1298. https://doi.org/10.1038/nature04131

Palagi, E. (2006). Social play in bonobos ( *Pan paniscus* ) and chimpanzees ( *Pan troglodytes* ): Implicationsfor natural social systems and interindividual relationships. *American Journal of Physical Anthropology*, *129*(3), 418–426. https://doi.org/10.1002/ajpa.20289

Palagi, E., & Paoli, T. (2007). Play in adult bonobos ( *Pan paniscus* ): Modality and potential meaning. *American Journal of Physical Anthropology*, *134*(2), 219–225. https://doi.org/10.1002/ajpa.20657

Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J. R., Walenz, B., Koren, S., Sutton, G., Kodira, C., Winer, R., Knight, J. R., Mullikin, J. C., Meader, S. J., Ponting, C. P., Lunter, G., Higashino, S., Hobolth, A., Dutheil, J., Karakoç, E., … Pääbo, S. (2012). The bonobo genome compared with the chimpanzee and human genomes. *Nature*, *486*(7404), 527–531. https://doi.org/10.1038/nature11128

Pusey, A. E., Pintea, L., Wilson, M. L., Kamenya, S., & Goodall, J. (2007). The Contribution of Long-Term Research at Gombe National Park to Chimpanzee Conservation. *Conservation Biology*, *21*(3), 623–634. https://doi.org/10.1111/j.1523-1739.2007.00704.x

Reichert, K. E., Heistermann, M., Keith Hodges, J., Boesch, C., & Hohmann, G. (2002). What Females Tell Males About Their Reproductive Status: Are Morphological and Behavioural Cues Reliable Signals of Ovulation in Bonobos ( *Pan paniscus* )? *Ethology*, *108*(7), 583–600. https://doi.org/10.1046/j.1439-0310.2002.00798.x

Riedel, J., Franz, M., & Boesch, C. (2011). How feeding competition determines female chimpanzee gregariousness and ranging in the Taï National Park, Côte d'Ivoire. *American Journal of Primatology*, *73*(4), 305–313. https://doi.org/10.1002/ajp.20897

Rilling, J. K., Scholz, J., Preuss, T. M., Glasser, M. F., Errangi, B. K., & Behrens, T. E. (2012). Differences between chimpanzees and bonobos in neural systems supporting social cognition. *Social Cognitive and Affective Neuroscience*, *7*(4), 369–379. https://doi.org/10.1093/scan/nsr017

Ross, C. T., & Pisor, A. C. (2025). Perceived inequality and variability in the expression of parochial altruism. *Evolutionary Human Sciences*, *7*, e3. https://doi.org/10.1017/ehs.2024.43

Sachs, J. L., Mueller, U. G., Wilcox, T. P., & Bull, J. J. (2004). The Evolution of Cooperation. *The Quarterly Review of Biology*, *79*(2), 135–160. https://doi.org/10.1086/383541

Samuni, L., Crockford, C., & Wittig, R. M. (2021a). Group-level cooperation in chimpanzees is shaped by strong social ties. *Nature Communications*, *12*(1), 539. https://doi.org/10.1038/s41467-020-20709-9

Samuni, L., Crockford, C., & Wittig, R. M. (2021b). Group-level cooperation in chimpanzees is shaped by strong social ties. *Nature Communications*, *12*(1), 539. https://doi.org/10.1038/s41467-020-20709-9

Samuni, L., Langergraber, K. E., & Surbeck, M. H. (2022). Characterization of *Pan* social systems reveals in-group/out-group distinction and out-group tolerance in bonobos.

*Proceedings of the National Academy of Sciences*, *119*(26), e2201122119. https://doi.org/10.1073/pnas.2201122119

Samuni, L., Mielke, A., Preis, A., Crockford, C., & Wittig, R. M. (2020). Intergroup Competition Enhances Chimpanzee (Pan troglodytes verus) In-group Cohesion. *International Journal of Primatology*, *41*(2), 342–362. https://doi.org/10.1007/s10764-019-00112-y

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888), 20181643. https://doi.org/10.1098/rspb.2018.1643

Samuni, L., Preis, A., Mundry, R., Deschner, T., Crockford, C., & Wittig, R. M. (2017). Oxytocin reactivity during intergroup conflict in wild chimpanzees. *Proceedings of the National Academy of Sciences*, *114*(2), 268–273. https://doi.org/10.1073/pnas.1616812114

Samuni, L., & Surbeck, M. (2023). Cooperation across social borders in bonobos. *Science*, *382*(6672), 805–809. https://doi.org/10.1126/science.adg0844

Sandel, A. A., & Watts, D. P. (2021). Lethal Coalitionary Aggression Associated with a Community Fission in Chimpanzees (Pan troglodytes) at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, *42*(1), 26–48. https://doi.org/10.1007/s10764-020-00185-0

Šimić, G., Tkalčić, M., Vukić, V., Mulc, D., Španić, E., Šagud, M., Olucha-Bordonau, F. E., Vukšić, M., & R. Hof, P. (2021). Understanding Emotions: Origins and Roles of the Amygdala. *Biomolecules*, *11*(6), 823. https://doi.org/10.3390/biom11060823

Staes, N., Stevens, J. M. G., Helsen, P., Hillyer, M., Korody, M., & Eens, M. (2014). Oxytocin and Vasopressin Receptor Gene Variation as a Proximate Base for Inter-and Intraspecific Behavioral Differences in Bonobos and Chimpanzees. *PLoS ONE*, *9*(11), e113364. https://doi.org/10.1371/journal.pone.0113364

Stimpson, C. D., Barger, N., Taglialatela, J. P., Gendron-Fitzpatrick, A., Hof, P. R., Hopkins, W. D., & Sherwood, C. C. (2016). Differential serotonergic innervation of the amygdala in bonobos and chimpanzees. *Social Cognitive and Affective Neuroscience*, *11*(3), 413–422. https://doi.org/10.1093/scan/nsv128

Surbeck, M., Cheng, L., Kreyer, M., Gort, G., Mundry, R., Hohmann, G., & Fruth, B. (2025). Drivers of female power in bonobos. *Communications Biology*, *8*(1), 550. https://doi.org/10.1038/s42003-025-07900-8

Surbeck, M., & Hohmann, G. (2013). Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (Pan paniscus). *Behavioral Ecology and Sociobiology*, *67*(11), 1767–1780. https://doi.org/10.1007/s00265-013-1584-8

Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos ( *Pan paniscus* ). *Proceedings of the Royal Society B: Biological Sciences*, *278*(1705), 590–598. https://doi.org/10.1098/rspb.2010.1572

Tan, J., Ariely, D., & Hare, B. (2017). Bonobos respond prosocially toward members of other groups. *Scientific Reports*, *7*(1), 14733. https://doi.org/10.1038/s41598-017-15320-w

Tan, J., & Hare, B. (2013a). Bonobos Share with Strangers. *PLoS ONE*, *8*(1), e51922. https://doi.org/10.1371/journal.pone.0051922

Tan, J., & Hare, B. (2013b). Bonobos Share with Strangers. *PLoS ONE*, *8*(1), e51922. https://doi.org/10.1371/journal.pone.0051922

Thompson, F. J., Marshall, H. H., Vitikainen, E. I. K., & Cant, M. A. (2017). Causes and consequences of intergroup conflict in cooperative banded mongooses. *Animal Behaviour*, *126*, 31–40. https://doi.org/10.1016/j.anbehav.2017.01.017

Titterton, J. (2022). *Deception in Medieval Warfare: Trickery and Cunning in the Central Middle Ages* (1st ed.). Boydell and Brewer Limited. https://doi.org/10.1017/9781800104747

Tokuyama, N., & Furuichi, T. (2016). Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Animal Behaviour*, *119*, 27–35. https://doi.org/10.1016/j.anbehav.2016.06.021

Tokuyama, N., Sakamaki, T., & Furuichi, T. (2019). Inter-group aggressive interaction patterns indicate male mate defense and female cooperation across bonobo groups at Wamba, Democratic Republic of the Congo. *American Journal of Physical Anthropology*, *170*(4), 535–550. https://doi.org/10.1002/ajpa.23929

Tokuyama, N., Toda, K., Poiret, M.-L., Iyokango, B., Bakaa, B., & Ishizuka, S. (2021). Two wild female bonobos adopted infants from a different social group at Wamba. *Scientific Reports*, *11*(1), 4967. https://doi.org/10.1038/s41598-021-83667-2

Tooby, J., & Cosmides, L. (2025). The evolution of war and its cognitive foundations. *Evolution and Human Behavior*, *46*(3), 106687. https://doi.org/10.1016/j.evolhumbehav.2025.106687

Vervafcke, H., De Vries, H., & Van Elsacker, L. (2000). Function and distribution of coalitions in captive bonobos (Pan paniscus). *Primates*, *41*(3), 249–265. https://doi.org/10.1007/BF02557595

Vigilant, L. (2007). Bonobos. *Current Biology*, *17*(3), R74–R75. https://doi.org/10.1016/j.cub.2007.01.021

Walum, H., Lichtenstein, P., Neiderhiser, J. M., Reiss, D., Ganiban, J. M., Spotts, E. L., Pedersen, N. L., Anckarsäter, H., Larsson, H., & Westberg, L. (2012). Variation in the Oxytocin Receptor Gene Is Associated with Pair-Bonding and Social Behavior. *Biological Psychiatry*, *71*(5), 419–426. https://doi.org/10.1016/j.biopsych.2011.09.002

Watts, D., & Mitani, J. (2001). BOUNDARY PATROLS AND INTERGROUP ENCOUNTERS IN WILD CHIMPANZEES. *Behaviour*, *138*(3), 299–327. https://doi.org/10.1163/15685390152032488

Watts, D. P., Muller, M., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*, *68*(2), 161–180. https://doi.org/10.1002/ajp.20214

White, F. J., & Wood, K. D. (2007). Female feeding priority in bonobos, *Pan paniscus* , and the question of female dominance. *American Journal of Primatology*, *69*(8), 837–850. https://doi.org/10.1002/ajp.20387

Williams, J. M., Oehlert, G. W., Carlis, J. V., & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? *Animal Behaviour*, *68*(3), 523–532. https://doi.org/10.1016/j.anbehav.2003.09.015

Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees’ ranging patterns. *Animal Behaviour*, *63*(2), 347–360. https://doi.org/10.1006/anbe.2001.1916

Wilson, M., Hauser, M., & Wrangham, R. (2007). Chimpanzees (Pan troglodytes) modify grouping and vocal behaviour in response to location-specific risk. *Behaviour*, *144*(12), 1621–1653. https://doi.org/10.1163/156853907782512137

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., Hobaiter, C. L., Hohmann, G., Itoh, N., Koops, K., Lloyd, J. N., Matsuzawa, T., Mitani, J. C., Mjungu, D. C., Morgan, D., Muller, M. N., Mundry, R., Nakamura, M., Pruetz, J., … Wrangham, R. W. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature*, *513*(7518), 414–417. https://doi.org/10.1038/nature13727

Wilson, M. L., Britton, N. F., & Franks, N. R. (2002). Chimpanzees and the mathematics of battle. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1496), 1107–1112. https://doi.org/10.1098/rspb.2001.1926

Wilson, M. L., Hauser, M. D., & Wrangham, R. W. (2001). Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour*, *61*(6), 1203–1216. https://doi.org/10.1006/anbe.2000.1706

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup Relations in Chimpanzees. *Annual Review of Anthropology*, *32*(1), 363–392. https://doi.org/10.1146/annurev.anthro.32.061002.120046

Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., & Zuberbühler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20133096. https://doi.org/10.1098/rspb.2013.3096

Wittig, R. M., Crockford, C., Langergraber, K. E., & Zuberbühler, K. (2014). Triadic social interactions operate across time: A field experiment with wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1779), 20133155. https://doi.org/10.1098/rspb.2013.3155

Wobber, V., Hare, B., Maboto, J., Lipson, S., Wrangham, R., & Ellison, P. T. (2010). Differential changes in steroid hormones before competition in bonobos and chimpanzees. *Proceedings of the National Academy of Sciences*, *107*(28), 12457–12462. https://doi.org/10.1073/pnas.1007411107

Wolf, D., Klasen, M., Eisner, P., Zepf, F. D., Zvyagintsev, M., Palomero-Gallagher, N., Weber, R., Eisert, A., & Mathiak, K. (2018). Central serotonin modulates neural responses to virtual violent actions in emotion regulation networks. *Brain Structure and Function*, *223*(7), 3327–3345. https://doi.org/10.1007/s00429-018-1693-2

Wrangham, R. W. (2018). Two types of aggression in human evolution. *Proceedings of the National Academy of Sciences*, *115*(2), 245–253. https://doi.org/10.1073/pnas.1713611115

Wrangham, R. W. (2019). Hypotheses for the Evolution of Reduced Reactive Aggression in the Context of Human Self-Domestication. *Frontiers in Psychology*, *10*, 1914. https://doi.org/10.3389/fpsyg.2019.01914

Wrangham, R. W., & Glowacki, L. (2012). Intergroup Aggression in Chimpanzees and War in Nomadic Hunter-Gatherers: Evaluating the Chimpanzee Model. *Human Nature*, *23*(1), 5–29. https://doi.org/10.1007/s12110-012-9132-1

Yamashita, K., & Kitano, T. (2013). Molecular evolution of the oxytocin–oxytocin receptor system in eutherians. *Molecular Phylogenetics and Evolution*, *67*(2), 520–528. https://doi.org/10.1016/j.ympev.2013.02.017

Yirmiya, N., Rosenberg, C., Levi, S., Salomon, S., Shulman, C., Nemanov, L., Dina, C., & Ebstein, R. P. (2006). Association between the arginine vasopressin 1a receptor (AVPR1a) gene and autism in a family-based study: Mediation by socialization skills. *Molecular Psychiatry*, *11*(5), 488–494. https://doi.org/10.1038/sj.mp.4001812

Young, S. N., & Leyton, M. (2002). The role of serotonin in human mood and social interaction. *Pharmacology Biochemistry and Behavior*, *71*(4), 857–865. https://doi.org/10.1016/S0091-3057(01)00670-0

Zhu, N., & Chang, L. (2020). An evolutionary life history explanation of sexism and gender inequality. *Personality and Individual Differences*, *157*, 109806. https://doi.org/10.1016/j.paid.2019.109806