AN-03 Great apes: four models of sex relations

The comparative study of extant great apes—chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla spp.*), and orangutans (*Pongo spp.*)—provides an indispensable empirical foundation for understanding the evolutionary trajectory of hominid social systems and sex relations. Because humans share a relatively recent common ancestor with these species, mapping their diverse anatomical, behavioural, and cultural adaptations clarifies the phylogenetic constraints and socioecological pressures that forged human sociality. This report systematically analyses the social systems of the four great ape models with respect to sex relations, dominance, female coalitions, sexual dimorphism, and mating systems.

To ensure analytical rigour, this analysis segregates the evidence into three distinct layers: physiology (measurable anatomical and neurobiological traits), behaviour (statistical distributions of actions and interactions), and culture (variable, socially transmitted intra-specific traditions). Furthermore, it evaluates the intense paleoanthropological debate regarding which ape serves as the most accurate referential model for the chimpanzee-human last common ancestor (LCA), contrasting orthodox chimpanzee-centric models with emerging fossil evidence.

Layer 1: Physiology (Measurable)

The physiological layer encompasses the quantifiable anatomical, morphological, and neurological structures that underpin great ape sex relations. These traits are heavily constrained by genetics and evolutionary history, reflecting millions of years of selective pressures related to intra- and inter-sexual competition.

Body Size and Canine Sexual Dimorphism

Sexual dimorphism in body mass and canine tooth size serves as a primary physiological indicator of the evolutionary history of male-male contest competition[1]. According to Plavcan (2001) in the *American Journal of Physical Anthropology*, dimorphism levels vary drastically among the great apes, correlating strongly with their respective mating systems and the intensity of male monopolisation of females[3].

Gorillas and orangutans exhibit the most extreme dimorphism. Relying on foundational morphometric data from Smith and Jungers (1997) in the *Journal of Human Evolution*, male gorillas weigh an average of 169.3 kg compared to the female average of 75.7 kg, yielding a male-to-female (m/f) body mass ratio of approximately 2.24[5]. Orangutans demonstrate a similarly high m/f body mass ratio of 2.19 to 2.23 (78.3 kg for males versus 35.8 kg for females), alongside extreme canine dimorphism[6]. In both genera, this extreme physiological divergence is the evolutionary consequence of intense pre-copulatory physical combat, where sheer physical bulk and large canines dictate success in violent, high-stakes contests for exclusive reproductive access.

Conversely, the *Pan* genus demonstrates markedly reduced physiological dimorphism. Chimpanzees possess an m/f body mass ratio of roughly 1.27 (42.7 kg to 33.7 kg), while

bonobos show a slightly higher but comparable ratio of 1.36[6]. Despite their reduced body size dimorphism relative to gorillas, both chimpanzees and bonobos retain significant canine dimorphism. The moderate body size dimorphism in *Pan* reflects a shift away from exclusive male-male physical monopolisation of females toward a mating system where multiple males mate with multiple females. Consequently, the arena of competition shifts away from sheer body mass toward post-copulatory physiological mechanisms.

Species	Mating System	M/F Body Mass Ratio	Canine Dimorphism	Relative Testis Mass
Gorilla spp.	Polygynous (Single/Multi-male)	~2.24	Extreme	Very Small
Pongo spp.	Semi-solitary / Promiscuous	~2.19 - 2.23	Extreme	Small
Pan troglodytes	Fission-fusion / Promiscuous	~1.27	Moderate	Extremely Large
Pan paniscus	Fission-fusion / Promiscuous	~1.36	Moderate	Very Large
Homo sapiens	Pair-bonded / Polygynous	~1.15	Minimal	Moderate

Testis Mass and Sperm Competition

The physiological hallmark of multi-male mating systems is macrorchidia (enlarged testicles), a direct adaptation to sperm competition. As demonstrated by Harcourt et al. (1981) in *Nature*, relative testis mass is highly predictive of female mating behaviour across primate species[8]. In chimpanzees, where estrous females routinely mate with multiple males, selection favours males capable of depositing the highest volume of high-quality sperm to outcompete rivals within the female reproductive tract[9]. Consequently, chimpanzee testes weigh between 150 and 170 grams, which is three to ten times larger than human testes (16–50 grams), despite humans possessing a 30% larger overall body mass[8]. Bonobos possess similarly enlarged testes, reflecting their highly promiscuous mating system. Histological comparisons further substantiate this: species with high sperm competition possess a 1.5 to 3 times higher proportion of seminiferous tubules (sperm-producing tissue) relative to interstitial tissue compared to single-male species[8].

In stark contrast, gorillas experience negligible sperm competition due to a social system

where a single dominant silverback typically monopolises reproductive access to a group of females. Consequently, gorillas exhibit severe erosion of the male reproductive system regarding sperm competition traits; they possess extremely small testes relative to their body mass, a low ratio of seminiferous tubules, and produce fewer, lower-quality sperm with lower swimming speeds[12]. Orangutans, who also experience limited sperm competition compared to *Pan*, similarly possess small testes[9].

Neurobiology and Socio-Emotional Circuitry

Physiological divergence extends deep into the neuroanatomy that regulates social behaviour. Despite separating from a common ancestor only 1 to 2 million years ago, chimpanzees and bonobos exhibit distinct neurobiological profiles. Rilling et al. (2012), publishing in the *Proceedings of the National Academy of Sciences (PNAS)*, utilised diffusion tensor imaging and voxel-wise analysis (sample size: n=4 bonobos, n=6 chimpanzees) to compare neural circuitry[14]. The structural neuroimaging revealed that bonobos possess significantly more gray matter in brain regions associated with perceiving distress in oneself and others, specifically the right dorsal amygdala and the right anterior insula[14]. Furthermore, bonobos exhibit a larger, more robust white matter pathway linking the amygdala with the ventral anterior cingulate cortex[15]. This specific pathway is heavily implicated in both the top-down cognitive control of aggressive impulses and bottom-up biases against harming conspecifics[15]. The physiological enhancement of these empathic and aggression-regulating circuits in bonobos provides a measurable anatomical substrate for their statistically lower rates of lethal violence and higher rates of tension-dissipating socio-sexual behaviour compared to chimpanzees. While the sample size of this neuroimaging study is inherently small due to the difficulty of scanning live apes, the effect sizes were significant, and the structural differences align seamlessly with observed species-typical behaviours.

Layer 2: Behaviour (Statistical, Overlapping Distributions)

The behavioural layer maps the statistical distributions of social interactions. Unlike binary physiological traits, behaviour operates on overlapping distributions, meaning intra-specific variation exists, but species-level averages and statistical probabilities reveal distinct evolutionary strategies regarding dominance, alliances, female dispersal, and violence.

Bonobo Female Coalitions and Dominance

In mammalian species with male-biased sexual dimorphism, male dominance over females is the statistical rule. Bonobos present a rare and highly debated exception. Wild bonobo females famously hold high social status, often outranking larger, stronger males and maintaining priority of access to feeding sites[16].

The exact mechanism underlying this female power was definitively quantified by Surbeck et al. (2025) in *Communications Biology*. The authors tested three competing models: the self-organisation hypothesis (where females win by default due to high male-male attrition), the reproductive control hypothesis (where concealed ovulation forces males into non-aggressive strategies), and the female coalition hypothesis (where females actively unite

to suppress males)[17]. The researchers analysed an exhaustive dataset encompassing 30 years of demographic and behavioural observations across six wild bonobo communities, capturing 1,786 intersexual conflicts[16].

The statistical results definitively supported the female coalition hypothesis and rejected the others. Females won 61% of dyadic conflicts with males (1,099 out of 1,786) and outranked 70% of males on average[16]. Crucially, the data demonstrated that female bonobos maintain this power not through individual physical strength, but through aggressive alliances. In 85% of all observed coalitions, females collectively targeted males, forcing them into submission through loud, highly coordinated attacks[16]. Generalized Linear Mixed Models (GLMMs) confirmed that the frequency of these female-female coalitions directly and significantly correlated with higher female rank and greater power over males[17].

The cohesion of these female networks is remarkably complex because, like chimpanzees, female bonobos disperse from their natal groups upon reaching maturity. Adult females in a community are unrelated immigrants. They overcome this lack of kinship through extensive socio-sexual behaviour, specifically genito-genital (GG) rubbing. Moscovice et al. (2019) in *Hormones and Behavior* demonstrated that GG-rubbing among female bonobos triggers a significant release of urinary oxytocin, a neuropeptide that enhances social bonding, proximity, and subsequent cooperation[22]. This behaviour occurs frequently during tense feeding contexts or post-conflict reconciliation, allowing unrelated females to forge the deep social bonds necessary to execute coordinated attacks against larger males[16]. This finding has successfully replicated across multiple bonobo populations, demonstrating that social support can entirely invert a physically determined power structure.

Chimpanzee Male Alliances, Territoriality, and Lethal Aggression

Chimpanzee behaviour is fundamentally structured around male philopatry (males remain in their natal groups) and male-bonded dominance hierarchies. Unlike bonobos, all adult male chimpanzees socially dominate all females, frequently utilizing sexual coercion[19]. However, the most defining behavioural divergence of chimpanzees is their propensity for lethal coalitionary aggression against conspecifics.

Chimpanzees exhibit a fluid fission-fusion social dynamic, where group members break into smaller foraging parties[26]. According to Wrangham's (1999) "imbalance of power" hypothesis published in the *American Journal of Physical Anthropology*, this fission-fusion ecology creates situations where a large patrol of males from one community can encounter a solitary individual or small party from a neighbouring group[28]. When the attackers hold a vast numerical advantage (typically a mean ratio of 8:1), they can kill the victim with near-zero risk of injury to themselves[28].

This behaviour is statistically robust and heavily replicated. A landmark meta-analysis by Wilson et al. (2014) in *Nature* reviewed data from 18 chimpanzee communities and 4 bonobo communities, encompassing 152 observed or inferred killings[29]. The fitness benefits of this violence are substantial. Mitani, Wood, and colleagues (2010, 2021) in *PNAS* demonstrated that the Ngogo chimpanzee community expanded its territory by 22% through the systematic killing of 13 neighbours over ten years. This territorial expansion resulted in a statistically significant

increase in female fertility and infant survivorship due to enhanced access to food resources[31]. The evolutionary origins of this behaviour are the subject of intense controversy. Critics of the adaptive view of chimpanzee warfare, most notably anthropologist R. Brian Ferguson and science writer John Horgan, argue that the data in Wilson et al. (2014) is skewed by sites with a history of human provisioning (like Gombe and Mahale) or habitat destruction[30]. Ferguson posits that chimpanzee lethal violence is a recent, non-adaptive response to artificial resource scarcity and human interference. However, Wilson and colleagues counter this forcefully: their *Nature* meta-analysis demonstrated that provisioning history and human impact metrics do not statistically explain the variation in killing rates among chimpanzee communities[30]. Lethal aggression has been widely documented in completely unprovisioned, undisturbed sites (like Ngogo and Goualougo), solidifying the consensus in primatology that proactive lethal aggression is an innate, adaptive chimpanzee behavioural strategy[30].

Gorilla Infanticide and Male Monopolisation

Gorilla social behaviour revolves around extreme male monopolisation of females. The dominant silverback male achieves reproductive success by protecting a harem of females from rival males[35]. Because male gorillas lack the sperm competition mechanisms of chimpanzees, their reproductive leverage is entirely dependent on retaining physical group dominance.

This dynamic yields high rates of infanticide by extra-group males or ascending subordinate males. When a male takes over a group following the death or defeat of the resident silverback, he routinely kills the unweaned infants of the resident females. This act prematurely terminates the females' lactational amenorrhea, bringing them back into estrus so the new male can sire his own offspring[35]. Robbins et al. (2013) in *PLoS One* analysed over 40 years of demographic data from mountain gorillas, encompassing up to 70% of the entire population[35]. They found that infanticide accounts for up to 21% of all infant mortality, representing a massive evolutionary pressure[35].

Consequently, female gorilla social decisions—including secondary dispersal (transferring between groups)—are heavily dictated by the need to find a silverback strong enough to protect her infants from infanticidal outsiders. Robbins et al. term this the "male strength model," wherein females must balance the risk of joining a single-male group (which carries a 57% infant mortality rate if the male is replaced) against the benefits of multi-male groups (which have only a 6% infant mortality rate during replacements, as subordinates step in to protect infants)[35].

Orangutan Bimaturism and Coercive Mating

Orangutan sex relations are characterised by an extreme and unique physiological-behavioural overlap known as male bimaturism[38]. Male orangutans develop into one of two distinct sexually mature adult morphs: flanged or unflanged. Flanged males develop large cheek pads, a throat sac for emitting long calls to attract females, and immense body size[38]. Unflanged males remain in a state of arrested development, resembling females in size and lacking secondary sexual characteristics, though they are fully capable of reproduction[38].

Behaviourally, these morphs deploy radically different reproductive strategies. Flanged males

operate a "sit-and-wait" strategy, using long calls to attract receptive females who preferentially choose to mate with them to secure protection from harassment[38]. Unflanged males, lacking the physiological traits to attract female choice, adopt a roaming strategy and frequently engage in forced copulations (sexual coercion)[38].

The success of these strategies depends heavily on the stability of the local dominance hierarchy. Genetic paternity data presented by Utami Atmoko et al. (2002) and Knott (2009) show that when a single dominant flanged male securely controls an area, he secures the vast majority of paternities[38]. However, during periods of rank instability among flanged males, the reproductive success of unflanged males increases dramatically as they circumvent the chaotic male-male contest competition to force copulations with females[38].

Layer 3: Culture (Variable)

The third layer, culture, encompasses the socially transmitted, site-specific variations in behaviour that overlay genetic and physiological predispositions. While biology sets the baseline parameters, local ecology, population density, and demographic histories dictate the exact expression of great ape sex relations.

Intra-specific variation is pronounced across all four species. For instance, the degree of female dominance in bonobos is not a rigid biological absolute but a culturally and ecologically mediated statistical reality. Surbeck et al. (2025) explicitly noted that female power varied considerably across the six studied communities and over time[16]. In some communities (such as Ekalakala and Bompusa West), specific males occasionally achieved the alpha position, often buoyed by the presence of a high-ranking mother acting as an ally[20]. Furthermore, captive studies traditionally reported absolute female dominance over all males, but the 30-year wild data reveals a much more nuanced continuum where males occasionally win conflicts[20].

Among chimpanzees, the cultural transmission of violence and territoriality is highly contingent on local ecology. The intensity of intergroup lethal aggression varies significantly depending on the distribution of food resources and population density[29]. Savannah-dwelling chimpanzees, which live in lower-density populations with widely distributed resources, historically showed lower rates of lethal aggression compared to forest-dwelling chimpanzees, supporting the hypothesis that reduced resource competition alters culture. However, recent observations by Piel and colleagues (2020) in *Primates* documented the first intercommunity killing by savannah chimpanzees in the Issa Valley, confirming that while culture modulates frequency, the innate capacity for lethal coalitionary aggression remains intact[29].

In gorillas, the cultural and demographic environment dictates group structure. While Western lowland gorillas primarily form single-male groups, roughly 40% of Mountain gorilla groups are multi-male[36]. The ecological abundance of terrestrial vegetation in the mountains allows for higher group cohesion, reducing the feeding competition that normally prevents multiple adult males from coexisting. This creates a cultural buffer against infanticide, though single-male groups with exceptionally strong silverbacks remain highly viable[35].

Evolutionary Debates: The Last Common Ancestor (LCA) and Human Nature

Determining which great ape provides the most accurate referential model for the chimpanzee-human last common ancestor (LCA)—and by extension, baseline human nature—is one of the most fiercely contested debates in paleoanthropology.

The Chimpanzee Referential Model and Its Critics

For decades, the orthodox consensus relied on the "Chimpanzee Referential Model." This model posits that because humans and chimpanzees both exhibit male kin-bonded societies, territoriality, and proactive lethal coalitionary aggression, these traits were almost certainly present in the LCA[32]. Wrangham's (1996) "Demonic Males" hypothesis suggests that the human propensity for warfare is an innate evolutionary inheritance derived from our shared ancestry with chimpanzees, driven by the imbalance of power and scramble competition[28].

However, this model has faced severe criticism. Sayers and Lovejoy (2008) in the *American Journal of Physical Anthropology* heavily critiqued the over-reliance on chimpanzees, arguing that bonobos—who share exactly the same phylogenetic distance from humans—are systematically ignored because their peaceful, female-dominated, and highly sexualised behaviour contradicts the narrative of innate hominid violence[45]. Sayers, Lovejoy, and Duda (2013) argue that chimpanzee violence and male dominance may be terminal autapomorphies (uniquely derived traits in the *Pan troglodytes* lineage) rather than ancestral retentions[45].

The Fossil Evidence: *Ardipithecus ramidus*

The discovery and subsequent analysis of *Ardipithecus ramidus* (a 4.4-million-year-old early hominid) has profoundly shifted the LCA debate. As detailed by Suwa, Lovejoy, and colleagues (2021) in *PNAS*, *Ardipithecus* provides a direct morphological window into early hominid sex relations[49].

Crucially, *Ardipithecus ramidus* exhibited negligible canine sexual dimorphism. The male-to-female canine size ratio was estimated at 1.06 to 1.13, placing it entirely within the modern human range of variation and rendering it significantly less dimorphic than even the peaceful bonobo[49]. Lovejoy (2009) and Suwa et al. (2021) argue that this drastic reduction in the male canine indicates a profound and ancient behavioural shift away from male-male agonistic competition and aggressive monopolisation[49]. The lack of biological weaponry in early hominid males suggests that the LCA was neither a chimpanzee-like warmonger nor a gorilla-like harem master, but rather a species characterised by high social tolerance, reduced intra-sexual violence, and potentially the early stages of pair-bonding[49].

The Evolution of Human Pair-Bonding and Exogamy

If the LCA was characterised by reduced male aggression, how did the unique human social structure—characterised by egalitarianism, marriage, and complex meta-group alliances—evolve?

Anthropologist Bernard Chapais, in his seminal 2008 book *Primeval Kinship: How Pair-Bonding Gave Birth to Human Society*, offers a synthesis. Chapais argues that human society bridges the gap between ape promiscuity and human complexity through the evolution of the sexual pair-bond within a multi-male/multi-female group[51]. While chimpanzee society is fractured by lethal inter-group boundaries, human evolution saw the development of reciprocal exogamy (the formal exchange of mates between kin groups)[52]. Pair-bonding allowed human ancestors

to recognise affinal kin (in-laws). This recognition transformed hostile neighbouring groups into allied networks connected by marriage, fundamentally suppressing the chimpanzee-style "imbalance of power" violence through strategic, cross-boundary social and economic alliances[53].

Averages vs. Individuals: The Nuance of Behaviour

When modelling human nature on great apes, it is vital to distinguish species-level statistical averages from individual behavioural plasticity. Averages describe evolutionary strategies; individuals demonstrate adaptive flexibility.

For example, while the average chimpanzee male is aggressively dominant, some males achieve high rank not through brute force but through extensive grooming and affiliative alliance-building. Similarly, while bonobos are defined by female coalitions and reduced lethal aggression, this dominance is "by no means the rule" in every individual interaction[16]. Surbeck et al. (2025) note that males can and do win 39% of conflicts against females, and the highest-ranking individual in several bonobo communities for certain years was a male[20]. In orangutans, unflanged males are statistically viewed as employing forced copulations, but individual unflanged males occasionally form cooperative consortships with females during periods of extreme rank instability[38]. Acknowledging this individual variation prevents biological determinism and highlights that ape social strategies are highly plastic responses to local demographic contexts.

Summary of Robust Findings

Great ape sex relations are profoundly shaped by physiological dimorphism; intense male-male contest competition in gorillas and orangutans is reflected in massive body and canine dimorphism, whereas high sperm competition in chimpanzees and bonobos is reflected in enlarged testis mass. Gorilla sociality is driven by male harem monopolisation, leading to high rates of infanticide by rival males, which accounts for 21% of infant mortality and dictates female dispersal decisions. Orangutans exhibit unique male bimaturism, where flanged males rely on female choice and unflanged males heavily utilize sexual coercion. Chimpanzee societies are strictly patriarchal and territorial, where male-male alliances facilitate adaptive, proactive lethal coalitionary aggression against neighbours to expand territory and increase female fertility. Conversely, bonobo societies are matriarchal, with female dominance maintained not by individual physical size, but by aggressive female-female coalitions that target males in 85% of instances. This female solidarity in bonobos is neurobiologically supported by enhanced empathic brain circuitry and socially cemented via GG-rubbing, which triggers oxytocin release among unrelated immigrant females. Finally, the orthodox model proposing a violent, chimpanzee-like ancestor for humans is severely challenged by fossil evidence from *Ardipithecus ramidus*, which shows minimal canine dimorphism, suggesting early hominids were defined by high social tolerance and the evolutionary onset of pair-bonding.

Contested or Open Questions

1. **The True Nature of the LCA:** Was the last common ancestor of *Pan* and *Homo* more

chimpanzee-like (violent, male-dominant), bonobo-like (tolerant, female-coalition based), or a unique physiological baseline analogous to neither?
2. **Anthropogenic Impact on Violence:** Despite robust statistical refutations, debate persists regarding the extent to which human-induced habitat fragmentation and historical provisioning may artificially exacerbate the baseline frequency of chimpanzee lethal intergroup aggression.
3. **Evolution of Bonobo Female Coalitions:** Why did female coalitions evolve to invert the dominance hierarchy in bonobos, but not in chimpanzees, despite their nearly identical phylogenetic origins and similar female dispersal patterns?
4. **Origins of Human Pair-Bonding:** Did hominid pair-bonding evolve primarily to ensure male provisioning of altricial offspring, to guard mates from rival males in dense social groups, or as a mechanism to prevent infanticide?
5. **Orangutan Bimaturism:** What specific genetic and endocrinological triggers determine whether a male orangutan will develop flanges or remain in a state of arrested development, and how is this modulated by the presence of a dominant male?

Most Important Sources to Read in Full

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Implications for Living Together

Drawing implications from great ape behaviour for human couples, families, and societies requires extreme caution to avoid the naturalistic fallacy—the erroneous assumption that because a behaviour is "natural" or evolutionarily ancient, it is therefore morally good,

inevitable, or desirable. Ape societies feature infanticide, sexual coercion, and lethal warfare; asserting these are natural evolutionary strategies does not render them acceptable blueprints for human ethics.

Instead, the comparative ape data reveals the *mechanisms* of social organisation. From bonobos, we learn that physical size asymmetries (which exist between human males and females) do not inevitably dictate male dominance; robust female social support networks and coalitionary solidarity are highly effective, evolved strategies for counteracting physical power imbalances and mitigating coercion. From chimpanzees, we observe that fission-fusion dynamics and rigid in-group/out-group boundaries reliably generate lethal conflict when an imbalance of power exists; human organisations and societies must actively design structural constraints and inter-group dependencies to prevent default factional violence.

Ultimately, human evolution—as modelled by the transition from ape promiscuity to reciprocal exogamy—demonstrates that our species' supreme adaptive advantage is not solitary dominance or insular warfare, but the capacity to forge cooperative, cross-boundary alliances. For couples, families, and organisations, this implies that stability is best achieved by continuously reinforcing cooperative networks, actively regulating power imbalances through coalitionary support, and formalising social ties that bridge disparate groups to foster mutual reliance.

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