

Regis University

ePublications at Regis University

Regis University Student Publications

Spring 2022

"Bonobo" rights for all: Using a primatological approach to secure gender equity

Francesca V.E. Kaser
Regis University

Follow this and additional works at: <https://epublications.regis.edu/theses>



Part of the [Biological and Physical Anthropology Commons](#), and the [Feminist, Gender, and Sexuality Studies Commons](#)

Recommended Citation

Kaser, Francesca V.E., "'Bonobo' rights for all: Using a primatological approach to secure gender equity" (2022). *Regis University Student Publications*. 1022.
<https://epublications.regis.edu/theses/1022>

This Thesis - Open Access is brought to you for free and open access by ePublications at Regis University. It has been accepted for inclusion in Regis University Student Publications by an authorized administrator of ePublications at Regis University. For more information, please contact epublications@regis.edu.

**“BONOBO” RIGHTS FOR ALL: USING A PRIMATOLOGICAL
APPROACH TO SECURE GENDER EQUITY**

**A thesis submitted to
Regis College
The Honors Program
in partial fulfillment of the requirements
For Graduation with Honors**

by

Francesca V.E. Kaser

May 2022

Thesis written by

Francesca V.E. Kaser

Approved by

Amy L. Schreier

Thesis Advisor

Michael J. Benedetto

Thesis Reader

Accepted by

Amy L. Schreier

Director, Regis College Honors Program

Table of Contents

ACKNOWLEDGEMENTS	1
LIST OF FIGURES	2
INTRODUCTION	3
I. WOMAN THE GATHERER	9
II. CHIMPANZEES: UNDERSTANDING MALE-DOMINANCE	19
III. BONOBOBOS: UNDERSTANDING FEMALE-DOMINANCE	27
IV. GIBBONS and SIAMANGS: UNDERSTANDING EGALITARIANISM	34
V. INTERSECTING PRIMATOLOGY AND FEMINIST THEORY	41
VI. WOMEN IN PRIMATOLOGY	50
CONCLUSION	53
LITERATURE CITED	57

Abstract

Name: Francesca Kaser Major: Biology

“BONOBO” RIGHTS FOR ALL: USING A PRIMATOLOGICAL
APPROACH TO SECURE GENDER EQUITY

Advisor’s Name: Dr. Amy L. Schreier

Reader’s Name: Dr. Michael J. Ghedotti

Western patriarchy sustains male-dominance and perpetuates gender inequity. While there have been great achievements toward gender equity, women are burdened to navigate a society that upholds male success. Equality offers individuals the *same* opportunities, but often falls short in delivering equal outcomes because of historic and systemic male privileges conserved by patriarchy. Equity, on the other hand, ensures that *fair* opportunities effect equal outcomes to rectify systemic injustices. To reconstruct women’s role in society, our closest living relatives, patriarchal chimpanzees (*Pan troglodytes*) and matriarchal bonobos (*Pan paniscus*), allow humans to compare the role of females in diverse primate social systems. Female-dominant bonobos utilize female coalitionary power to actively suppresses male dominance. Ultimately, female power allows these “hippie apes” to maintain peace. Using an inter-disciplinary approach of primatology and feminist theory, I argue that female-dominance – as observed in bonobos – promotes relational feminism, whereby women, whose perspectives are shaped by patriarchal oppression, hold significantly more power to foster equitable treatment of people regardless of their gender. Increased rates of sociosexual behavior, female coalitionary support, and affiliative intersexual relationships in matriarchal bonobos should encourage Western people to consider an imperative transformation toward female dominance.

Acknowledgments

I send many thanks to my friends and family who have supported me throughout my thesis journey. The resilient women in my life have listened to me babble through convoluting ideas about female dominance, conversed about the ways in which we experience gender inequality, and discussed how we as a community can move forward to combat androcentrism. And through community, the Regis College Honors Program has helped me cultivate a passion for learning. My persistent pursuit of knowledge has been challenged and nurtured by my Honors cohort and professors. Thank you to the friends who have affected the trajectory of my thesis research.

I would also like to thank my reader, Dr. Mike Ghedotti, for offering invaluable insight in my search toward understanding female-dominance. Through the midst of battling yet another hectic year, he never failed to send me thoughtful feedback on my rough draft. Thank you for supporting me in this experience.

Finally, I send gratitude to my advisor, Dr. Amy Schreier. Not only has she helped me find nuance to my developing thesis argument and offered great advice, but she continues to motivate me to learn for the sake of knowledge itself. Dr. Schreier models that women primatologists foster equity in their scientific discipline. She shows that primatologists share a deep love for the animals they study. Thank you for playing a formative and encouraging role in my realization of the fascination I hold for nonhuman primates, particularly, the charming female-dominant bonobos.

List of Figures

- FIGURE 1: Activity budgets of captive same-species pair (*S. syndactylus*) 36
and mixed-species pair (male *N. gabrielle*, female *S. syndactylus*) at Denver
Zoo, Denver, CO.
- FIGURE 2: Spatial proximity of captive same-species pair (*S. syndactylus*) 37
and mixed-species pair (male *N. gabrielle*, female *S. syndactylus*) at Denver
Zoo, Denver, CO.

Introduction

“Nothing in life is to be feared, it is only to be understood. Now is the time to understand more, so that we may fear less” (Curie).

Today, most modern humans live in male-dominated societies with systemic gender inequality (Lorber, 2001). However, there are cultural groups that are exceptions to patriarchy’s modern persistence, including but certainly not limited to, the !Kung hunter-gatherers (Graeber & Wengrow, 2021), the Bantu Matrilineal Belt in south-central Africa (Robinson & Gottlieb, 2021), and the matrilineal Mósuō in China (He et al., 2016). In the history of Western patriarchy, there has been a gendered division of labor, with men’s domination of leadership positions and women’s acquiescence of domestic roles. This gendered division of labor leads to the assumption that men are superior to women because men monopolize positions of power (Parker & Parker, 1979). Even the “father of evolution,” Charles Darwin, claimed,

The chief distinction in the intellectual powers of the two sexes is [shown] by man attaining to a higher eminence, in whatever he takes up, than woman can attain—whether requiring deep thought, reason or imagination, or merely the use of the senses and hands... Thus, man has ultimately become superior to woman (1871).

And while Darwin may have been a “man of his time,” resistant to the women’s suffrage movement in England gaining momentum in 1867 just four years prior to his claims (Turner, 1913), his comments comparing men’s so-called “superiority” to women derives from his Victorian misogyny, not biological theory.

Feminist scholar Gerda Lerner defines patriarchy as, “the manifestation and institutionalization of male-dominance over women and children in the family and the extension of male-dominance over women in society in general” (1986, p. 239). Because patriarchal

organization manipulates and shapes a gendered division of labor, there is a historical gendered bias towards male researchers in the biological sciences. The research questions they subsequently propose are often male-centered. Therefore, it is not surprising that Darwin, a white heterosexual man privileged by Western patriarchy, believed that women were intellectually inferior because he worked with so few women.

The false perception of women's intellectual inferiority, however, is not due to biology, but rather society's failure to create intellectual spaces for women. During the Victorian era, women, who knew Darwin's claims were false, lacked the societal and political power to challenge Darwin and his male peers. For example, women who did oppose Darwin, notably Antoinette Brown Blackwell, who responded to Darwin's sexist claims in her book *The Sexes Throughout Nature*, were ignored by society. Blackwell (1875) contested that Darwin's assumptions about gender differences relied on non-biological human gender roles.

Today, however, primatology, a female-dominated field, has burgeoned in fostering an equitable discipline that cultivates cumulative knowledge (Strum & Fedigan, 2000). The pioneers of primatology are women, notably Jane Goodall, Dian Fossey, and Biruté Galdikas. Their gender also influences the questions they ask; they focus their studies on the role of females in primate societies. As powerful women, they promote diverse and international perspectives, as living non-human primates are found only in Africa, Asia, and Central and South America. Primatology challenges Darwin's Victorian misogyny because it models that female power leads to broader and representative knowledge.

Darwin attempted to defend his sexism with his theories of natural selection and sexual selection (Rosenthal & Ryan, 2022). Darwin's theory of natural selection is defined as differential reproduction based on heritable characteristics for a particular environment (Darwin,

1859). In other words, natural selection produces individuals that are well-adapted to their environment. By the process of sexual selection, traits are selected that increase an organism's ability to outcompete members of the same sex or make them more attractive to members of the opposite sex (Darwin, 1859). Female choice, subtle may it seem, is critical for her own reproductive success (Small, 1992). Darwin (1871), who recognized that female mammals are choosier when selecting mates, labeled females as “coy” and males as “eager.” While Darwin realized the importance of female agency (Prum, 2017) and promiscuity (Firman et al., 2017) in his theory of sexual selection, he repudiated this same capacity for his own species (Rosenthal & Ryan, 2022). Furthermore, to survive in Western patriarchy, women must sacrifice parts of their autonomy. In Western cultures, female mate choice is compromised by male power (Small, 1992).

Darwin's labels of “coy” females and “eager” males are based on parental investment. Parental investment theory states that the sex that invests more in its offspring will be the choosier mate (Trivers, 1972). Male pipefish and seahorses (Syngnathidae), for example, have high paternal investment and are the “choosier” sex because males carry the deposited eggs from the female. However, the opposite is true for mammals, whereby male reproductive success is controlled by access to fertile females, and females – who bear the energetic costs of reproduction (e.g., produce eggs, long periods of gestation and lactation) – have high maternal investment and are “choosy” (Trivers, 1972). In mammals, female reproductive success is therefore limited by her access to high quality food resources (Trivers, 1972). Today, though, based on human social capacity and modern technology, reproductive investment can be shifted, especially when one considers people who are in queer relationships who do not prescribe to heteronormativity.

Generally, sociobiologists argue that sexual selection and parental investment theory explain male dominance over females (Emlen & Oring, 1977; Wilson, 2000). But by defining females as “coy,” Darwin implies that male-dominance over females naturally persists in modern human cultures (Darwin, 1871). However, all animals, in some way or another, show exceptions to biological theory (Wilson, 2000). Therefore, biological theory cannot be universally applied to human social behavior.

Patriarchy persists not through biological determinism, but through widespread control of female sexuality (Small, 1992), whether that be a conscious decision by individual men to oppress women, or the social structures and patriarchal institutions that perpetuate women’s subordination. Western women have not “chosen” oppression but have sought mates who can offer resources and parental care despite systemic oppression (Small, 1992). Furthermore, women who live in patriarchal societies are structurally disempowered by male-dominated economic, political, and religious institutions (Lorber, 2001). Examining diverse social systems in closely related nonhuman primates, such as male-dominance, female-dominance, and egalitarianism, offers Western women insightful alternatives to their struggle against systemic gender inequality.

Among all primates, humans, a species of great ape belonging to the family Hominidae, are most closely related to chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), with whom we share more than 98% of our genetic material (Kovalaskas, Rilling, & Lindo, 2021). The last common ancestor of the genus *Pan* (which includes chimpanzees and bonobos) and *Homo* (which includes modern humans and our extinct hominin ancestors) lived between eight and four million years ago (Tocheri et al., 2008). Humans study nonhuman primates to understand the evolution and behavior of our own species (*Homo sapiens sapiens*). And because

chimpanzees and bonobos are most closely related to us, we can often make analogous assumptions about our evolutionary past (Knauff et al., 1991).

Chimpanzee social systems are male-dominant with male coalitions while bonobos are female-dominant with female coalitions (Kovalaskas, Rilling, & Lindo, 2021). Because both male chimpanzees and men primarily exhibit lethal aggression (Wrangham & Peterson, 1996), chimpanzees have often been central to understanding our violent evolutionary past. In humans, the persistence of violence against women, such as rape, sexual assault, and domestic violence (Hunnicut, 2009), I argue, has been legitimized by the “demonic male” origin story of both humans and chimpanzees (Wrangham & Peterson, 1996). Sustaining a male-dominance narrative justifies and excuses male violence. However, female-dominant bonobos, who frequently engage in sociosexual behavior to diffuse tension, indicate an alternative evolutionary path, devoid of lethal aggression (Wilson et al., 2014). Bonobos model that strong female coalitions avert male aggression and promote active, essential female power in society (Parish & de Waal, 2000).

Alternatively, egalitarian social systems, as observed in gibbons and siamangs (Hylobatidae) certainly offer prospects of gender equality (Graeber & Wengrow, 2021; Woodburn, 1982). Gibbons and siamangs are lesser apes with whom humans shared a common ancestor twenty to sixteen million years ago. Like the monogamous social organization that many presume for humans (Fuentes, 1998), individuals form nuclear family units, comprising the socially monogamous, pair-bonded adult male and female and their dependent offspring (Mootnick et al., 2006). Surely, in Western cultures, equality offers individuals the *same* opportunities and is especially important in sexual relationships. However, equality often falls short in delivering equal outcomes because of historic and systemic male privileges conserved by

Western patriarchy. Equity, on the other hand, ensures that *fair* opportunities effect equal outcomes to rectify systemic injustices (Cook & Hegtvedt, 1983).

Some Western people assume that humans have already reached a state of social gender equality (Launius & Hassel, 2018). Yet feminists' persistent activism indicates that Western cultures have not yet reached gender equality (Launius & Hassel, 2018). Therefore, a transition from patriarchy to egalitarianism, as seen in gibbon and siamang societies, is not radical enough to promote true gender equality. Moreover, Westerners should strive for an equitable, as opposed to equal, state based on fairness rather than universal sameness. A society marked by women's active participation, one that places females in positions of power, as we see in bonobos, is critical to reach an equitable and just state.

Essentially, systemic gender inequity is ingrained in Western patriarchal society (Becker, 1999). However, nonhuman primates offer humans the opportunity to compare sex roles in diverse social systems. Using an inter-disciplinary approach of primatology and feminist theory, I seek to answer questions regarding *how* and *why* patriarchy arose and suggest ways in which behaviors of the female-dominant bonobo offers prospects of gender equity in Western society.

CHAPTER I: Woman the gatherer

“Just imagine that we had never heard of chimpanzees or baboons and had known bonobos first. We would at present most likely believe that early hominids lived in female-centered societies, in which sex served important social functions and in which warfare was rare or absent” (de Waal, 1995, p. 7).

Control over female sexuality restricts women in nearly all aspects of their lives (Richardson, 1993). For example,

“It may influence the way [they] feel about [their] bodies and [their] appearance, the clothes [they] wear, the work [they] do, [their] health, the education [they] receive, and [their] leisure activities, as well as the relationships [they] feel able to have with both women and men” (Richardson, 1993, p. 75).

In this regard, men ultimately control *how* women express themselves. Women, therefore, are not truly free under a patriarchal system.

Furthermore, gender inequality influences economic agency. Women suffer from greater, more extreme rates of poverty (Chant, 2006). Women who live in male-dominated societies lack support from social institutions that are structured centered around the successes of men. The gendered division of labor, marked by gender-based disparities in economic, political, education, and health-related domains (Hausmann, 2009), exacerbates women’s economic injustice in patriarchal societies. So long as this injustice is neglected, the gender gap of relative inequality increases.

While there have been improvements in reducing the gender gap, especially in wealthy countries (Hausmann, 2009), the gap persists largely because women still struggle to hold positions of power and authority (Eagly & Carli, 2007). While the concrete wall first limited

women to work inside of the home, the glass ceiling allowed women the equal opportunity to obtain job positions outside of the home but were discouraged and excluded from leadership roles. However, women now exist in a labyrinth: there is a path to the top, but there are too many obstacles to *get* there (Eagly & Carli, 2007). It is imperative that this labyrinth be dismantled so that women can gain political power and hold leadership positions to advocate for gender equity.

Not all modern humans, and especially not early human hunter-gatherers, live in a patriarchal society. In early human history, women likely held leadership positions in hunter-gatherer societies (Lee, 1974). Although men's political dominance is extensive (Lorber, 2001), there is significant research on living hunter-gatherers, including the Inuit, !Kung of Kalahari, and Indigenous Australians, that contradict the assumptions that male political power originated in early human hunter-gatherers (Lee, 1974). Women in modern hunter-gatherer groups play a major economic role by providing most of their group's caloric diet, like plant foods, shellfish, and fish (Lee, 1974). However, men contribute to only a fraction of the diet (except in regions, like the Arctic, where they rely heavily on meat). Therefore, women can independently sustain their own diet. Historically, their essential economic role as a gatherer likely afforded them crucial political power (Lee, 1974).

Furthermore, the woman's family must approve marriages between men and women in hunter-gatherer societies (like the !Kung: Lee, 1974). Husbands, who are often ten years older than their wives, must prove themselves capable of hunting and ritual practices. Because girls are married between the ages of 15 to 25, to protect their daughter and oversee that her husband treats her well, the maternal parents require that the couple live in their home (Lee, 1974). In this familial structure, not only are mother-daughter bonds important, but so are bonds between brothers-in-law whom the maternal family "recruits" to aid in hunting efforts.

Each male and female, based on both kin and non-kin relationships, play a significant role in the political life of hunter-gatherers (Lee, 1974). Consequently, it is likely that early humans did not live in fixed androcentric societies. Ultimately, scientists can only predict ancestral behaviors by studying modern hunter-gatherers, for behavior, unlike bones and tools, is not fossilized. Due to the lack of complete evidence of early hunter-gatherers, assumptions about the nature of early human societies can never be established with absolute confidence (Lee, 1974). Moreover, any hunter-gatherer data used to promote the male-dominance origin narrative should be met with skepticism (Lee, 1974).

Within their predominantly egalitarian societies, particularly marked by social monogamy, high mobility, and lack of resource storage, early nomadic hunter-gatherers are considered highly cooperative (Lewis et al., 2014). Based on an agent-based simulation of early nomadic hunter-gatherers, humans thrived because of reliance on demand sharing cooperation, typically food sharing (Lewis et al., 2014). Based on reciprocity, demand sharing encourages individuals with highly coveted resources (like meat) to share with all group members, including individuals who don't contribute, such as free riders (Lewis et al., 2014). Classic economic games, such as N-Player Prisoner's Dilemma and the Hawk-Dove Game, show that while the "everybody hunts" model has higher payoffs than the "nobody hunts" model, the "everybody hunts but me" model has the highest payoffs for free riders (Lewis et al., 2014). However, these models exclude free riders who require sharing to survive, including adolescents with longer periods of growth and elderly who cannot physically hunt and gather but are important caregivers to grandchildren. Free riders are often family members.

Kin selection facilitates altruistic behavior (Eberhard, 1975). Kin selection and altruism are explained by inclusive fitness, or reproductive success, whereby an individual reduces their

individual fitness to promote their relative's fitness and increase their overall fitness (Eberhard, 1975; Quellar, 1992). Free riders, who rely on and extend altruistic behavior, are thus not evil, lazy people; they are essential to the functioning of humanity.

Human children require far longer periods of parental care than other young apes. Elderly relatives increase inclusive fitness by assisting in raising their grandchildren (as demonstrated by the grandmother effect: Chapman et al., 2019). In these nomadic hunter-gatherer groups, each person plays a crucial role in the survival of the group, whether that be through gathering food to feed others or providing extra care for the grandchild. Mobile hunter-gatherers relied on their relationships with one another to endure unpredictable circumstances associated with hunting and foraging (such as food shortages, illness, changes in weather, etc.: Page et al., 2017). Compared to loners, mobile families with longer life histories prompted the evolution of grandmothers (Lewis et al., 2014).

Despite relatively peaceful intragroup interactions within the numerous family units, male violence was still present in early human societies (Knauff et al., 1991; Wrangham & Peterson, 1996). And while some emphasize the importance of intergroup aggression to facilitate intragroup cooperation (Wrangham & Glowacki, 2012; Tokuyama, Sakamki, & Furuichi, 2019), the agent-based simulation of early nomadic hunter-gatherers indicates that fluid co-residence patterns among males and females and hyper-cooperative egalitarian social systems evolve in the absence of both punishment and warfare (Lewis et al., 2014).

If pre-agricultural society had relative equality between the sexes, how and why did patriarchy arise? Patriarchy likely originated before the introduction of agriculture, when males sought to control resources needed by women to reproduce. This enabled the transformation from male-dominated, male-philopatric primate societies to absolute patriarchy (Hrdy & Judge,

1993). Patriarchy optimizes male reproduction and allows men to control women's sexuality (Hrdy, 1997). Ultimately, patriarchy persists in modern Western society because men in power reap greater economic and social benefits when they uphold ultimate political power.

The systematic coercion and violence that emerged in modern humans due to socioeconomic disparities and a gendered political hierarchy is largely tied to the ability to store food surplus and greater food production (Knauff et al., 1991). Essentially, people stopped foraging, settled onto territory, and relied on agriculture to produce food that could be stored for long periods of time. Groups had greater incentive to protect the land they occupied. Because men are more likely to be fighters (Knauff et al., 1991), society valued men's role as aggressors and diminished women's role to focus solely on domestic work. That is not to say that women's role as domestic caretakers is unimportant, but that society served the successes of violent, aggressive men.

Knauff and colleagues (1991) suggest that male status in the evolutionary timeline is U-shaped rather than linear. Essentially, at one-point male status was an important factor to ancestral human group dynamics, then decreased during the hunter-gatherer Paleolithic era, before returning once agriculture allowed men to control food resources (Knauff et al., 1991). Furthermore, male status in humans and other great apes may be analogous rather than homologous, meaning that social systems may share a similar function but are not necessarily related to each other nor share an evolutionary origin (Knauff et al., 1991). So, researchers should certainly study the evolution of early human social groups to understand human behavior but should not attribute great significance to the rise of male-dominance and subsequent patriarchy because humans continue to evolve. Rather, it may be more important to recognize

Western culture's patriarchal similarities with chimpanzees while also aiming to change the evolutionary trajectory towards organizing into more equitable societies.

Egalitarianism is the most "equal" social system. And while egalitarianism can offer hope to solve gender inequality, equitable matrilineal societies who trace descent through maternal ancestry successfully bridge the gender gap by actively promoting female empowerment within their community. In matrilineal societies, most altruistic behaviors are directed toward matrilineal kin (Holden & Mace, 2003). Among matrilineal groups, resources are effectively shared among women rather than men, thus providing women with economic support to ultimately achieve a higher, more influential role in society. Matrilineal societies value female choice and women power because women are the primary investors to their offspring. Men from matrilineal societies, therefore, have little control over women's sexuality.

Among modern humans, matrilineality is rarer than patrilineality (descent through paternal ancestry and associated with the rise of patriarchy: Joseph, 1996). However, matrilineal descent, while most prevalent in Africa, persists in every region of the world (Robinson & Gottlieb, 2021). Among mammals, maternity is definite, but paternity could be uncertain. It is hypothesized that all African societies were originally matrilineal. Though, these groups later declined into patrilineal societies, possibly to control women's sexuality for paternal certainty, or for males to reap the benefits of male inheritance by utilizing male violence (Robinson & Gottlieb, 2021).

Additionally, imposed colonial, capitalist, and Christian ideologies (all patriarchal institutions) challenged the validity of matrilineality and replaced its structure with patrilineal descent (Phiri, 1983; Schatz, 2002). Today, matrilineal societies persist in south-central Africa, concentrated in a region known as the "Bantu Matrilineal Belt," around the Zambezi River

(Robinson & Gottlieb, 2021). Conversely, within matrilineal societies, where females remain in their natal group and males disperse to their wife's natal group, the avunculate, or maternal uncle, ultimately holds authority for making decisions within the maternal family unit (Robinson & Gottlieb, 2021).

Most matrilineal societies are matrilineal (He et al., 2016). With true decision making lying with the avunculate in matrilineal groups, the key difference between matrilineal societies with matrilineal residence and patrilineal societies with patrilineal residence, where the female resides with the male's family, is ultimately who the man controls: his sister and her children or his wife and his children (Robinson & Gottlieb, 2021). In matrilineal societies, most often inheritance is transferred from maternal uncle to son. However, in duolocal residence, in which the partners reside in separate households with their respective maternal families, one generation of matrilineal relatives collectively inherit their wealth from their mother's generation.

Comparatively, the Mósuō of China, another matrilineal group, are duolocal. The ancestral tribe of the Mósuō, Maoniu Quang, a branch of the Di-Quang group, migrated to southwest China about 2,700 years ago (You, 1997; He, 1999). Today, around 1,500 Mósuō people live around the Lugu Lake located in the northwestern province of Yunnan (Wen, 2004). Among the Mósuō, the women do nearly everything related to work: contribute shared household income, provide childcare, and harvest food to feed their family (He et al., 2016). While women are highly valued in this society, from an outsider's perspective, their roles are almost a form of glorified homemakers because, like in patriarchal groups, domestic labor comprises most women's responsibilities. While men traditionally trade, hunt, and fish, within the Mósuō community, women ultimately invest in more work than men by performing most of the subsistence farm work and housework (He et al., 2016).

Typically, duolocality is associated with male-biased investment because female offspring are in reproductive competition with mothers. However, the opposite is observed in the Mósuō community with daughter-biased investment being more common (He et al., 2016). Because females invest more in their offspring, to promote the offspring's survival, the grandmother supports her daughter as a mother more so than her son as a father. In this group, fathers play little to no role in their children's upbringing. Male reproductive success is not dependent on their natal household, but rather the traits of their partner's household (Ji et al., 2013).

Therefore, the matriliney-as-daughter-biased-investment (MDBI) hypothesis suggests that benefits of wealth to daughters are greater than benefits of wealth to sons. Furthermore, due to kin selection, female reproductive success is strengthened by a mother's encouragement to have children earlier and enhance the survival of her daughters' offspring (i.e., further support for the grandmother effect: Lewis et al., 2014). While Mósuō mothers help both sons and daughters, as grandmothers, they only assist with rearing their daughters' children due to the absence of paternal care. There is greater male dispersal after a mother's death compared to female dispersal, suggesting that once the mother dies, males lose benefits of living in their natal household (He et al., 2016). This specific duolocal matrilineal group therefore has different conditions acting on and influencing reproductive success compared to other matrilineal groups.

Mothers lack biparental care because of the Mósuō's non-monogamous mating system (He et al., 2016). In humans, male reproductive success is controlled by access to females, but female reproductive success is controlled by access to resources (Trivers, 1972). Adults undergo a walking marriage, a promiscuous mating system that contains no legal contract nor implied

paternal responsibility (Mattison, 2011). Within this promiscuous society, male reproduction is dependent on the female with whom they share a walking marriage. In addition to the absence of paternal care, paternal certainty doesn't impact female reproductive success. Women therefore control their own sexuality. From the Mósuō's perspective, mothers can depend on their family for child support and rely on a walking marriage not only as a source of reproduction but also pleasure.

From a sexual selection perspective, males increase their reproductive output by mating with multiple females, not just one single female as marriage implies (He et al., 2016). Walking marriages regulate males' access to females, and the diffusion of parenting within a matrilineal households ensure females' access to resources (He et al., 2016). Therefore, social sex, or sociosexual behavior, represented by a walking marriage in the Mósuō, prioritizes both physical pleasure and reproduction to strengthen social bonds and optimize reproductive success. Sex ultimately serves multiple social functions outside of reproduction. Within this community, sexual permissiveness is valued.

Matrilineal and egalitarian hunter-gatherer human societies have persisted and thrived outside of Western patriarchal intervention for thousands of years (Graeber & Wengrow, 2021; He et al., 2016; Lee, 1974; Mattison, 2011; Robinson & Gottlieb, 2021). Matrilineal societies are especially important to study because they exhibit a female-dominant-like human culture, and that cultural tradition profoundly impacts the ways in which women are valued in society. However, modeling modern human matrilineal and egalitarian societies is insufficient to achieve gender equity in Western civilization because it would require people to completely alter their economic practices. In an ideal world, Westerners should model matrilineality, but realistically in an established capitalistic society, this transition would be near impossible.

Furthermore, men maintain their power and suppress equity by justifying their aggressive behavior as derived from evolution, which has led to war, sexism, and violence against women (Wrangham & Peterson, 1996). Based on this interpretation of human evolution, men have thus been labeled “demonic males” (Wrangham & Peterson, 1996). Consequently, scientists have studied chimpanzees (*Pan troglodytes*) to understand human nature (Strum & Fedigan, 2000), but also to justify human aggression (Wrangham, 1999). However, women primatologists who investigate female reproductive strategies in primates find that “demonic males” are less central to primate societies than previous male scientists implied (Strum & Fedigan, 2000).

Within the genus *Pan*, which includes chimpanzees and bonobos (*Pan paniscus*), males incite and execute more aggression than females (Wilson et al., 2014). It is thus reasonable to compare male aggression between *Pan* and *Homo*, considering that among humans, men are more violent than women (Wrangham & Peterson, 1996). Certainly, both male violence and cooperation are important in the study of chimpanzees. But it is worthy to note, that these behavioral connections to the nature of androcentrism in humans be reviewed with reservation, for its implications may unconsciously assert a “male-dominated” agenda (Lee, 1974). Until 1929, bonobos weren’t recognized as a distinct species and were classified as “pygmy chimpanzees.” And while it may be more difficult to study bonobos due to their isolated geographic home range and small populations, one must examine the lack of their historical research and consider why bonobos have been “the forgotten ape,” possibly because of their female-centered and equitable society that substitutes sex for aggression (de Waal, 1995).

CHAPTER II: Chimpanzees: Understanding male-dominance

“Chimpanzees were a model for man; their natural family life, occurring just on the other side of the border from culture, was a mirror and testing ground for theories and policies” (Strum & Fedigan, 2000, p. 410).

Humans study chimpanzees (*Pan troglodytes*) to better understand human evolution. Chimpanzees are like humans in their anatomy (Lancaster, 1968) and behavior, including tool-use and toolmaking (Goodall, 1964), self-control (Osvath & Osvath, 2008), use of symbolic language (Hutchins, 2008), and culture (Goodall, 1964; McGrew, 1992). In many ways, chimpanzees humble our egotistical view that humans are superior to other nonhuman animals because they also possess “human-like” intelligence (Shepherd, 1915; Povinelli & Vonk, 2003; Bearzi & Standford, 2010).

Studying aggression among chimpanzees has helped scientists better understand how human aggression manifests. Studies suggest that proactive and reactive chimpanzee aggression can be comparable to human aggression (Wrangham, 1987; 1999; 2018). The contrasts of chimpanzee intelligence and aggression are neither good nor bad, but researchers must use caution when making comparisons between chimpanzee aggression and human aggression. For example, chimpanzee males who sexually coerce females sire more offspring than non-aggressive males (Feldblum et al., 2014). This suggests that aggression increases male reproductive success. The emphasis on the similarities between chimpanzee aggression and human aggression are potentially negative when used to justify, defend, and maintain male dominance in modern human society.

Chimpanzees live in multimale-multifemale, fission-fusion groups with promiscuous mating patterns, male-dominance hierarchies, and subordinate females (Grueter, Chapais, &

Zinner, 2012). Chimpanzees range across Africa, from Senegal and Gambia in the west to Uganda and Tanzania in the east (Gagneux et al., 2001). Females have slow rates of reproduction and provide all aspects of parental care (Pusey & Schroepfer-Walker, 2013). Chimpanzees are male philopatric, meaning males remain in their natal territory throughout life and females emigrate into new groups at sexual maturity to reduce chances of inbreeding (Pusey & Schroepfer-Walker, 2013). Adult males that remain in the group are thus largely related to one another. Subsequently, these related males form kinship coalitions. To protect their natal territory and strengthen their dominance over neighboring chimpanzee communities (Wrangham, 1999), they rely on affiliative and cooperative behaviors to maintain their power (Mitani, Merriweather, & Zhang, 2000). The relationships they share with other males affects their relative rank and consequent mating success (Gilby et al., 2016). Dynamic rank relationships cause frequent shifts in male rank (Foerster et al., 2016).

Dominance rank positively influences male reproductive success (Klinkova et al., 2005; Newton-Fisher et al., 2010; Bray, Pusey, & Gilby, 2016). Alpha males are typically more aggressive and have a higher probability of siring more offspring than males with lower rank (Wroblewski et al., 2009). Males who seek to increase their rank may benefit from escalated aggressive interactions with other males. By gaining higher rank, they increase their access to fertile females (Pusey et al., 2008) and have greater long-term reproductive success even after the hierarchy has shifted (Newton-Fisher et al., 2010). This implies that their prior social status has a lasting effect on mating strategies. Furthermore, forming strategic alliances benefit individuals who challenge the present rank (Foerster et al., 2016). Males with greater social connections in the hierarchy are observed to sire more offspring than males of similar rank (Gilby et al., 2016).

In a study of aggression among chimpanzees, 92% of attackers were male, 73% of victims were male, 66% of lethal aggression occurred between communities (e.g., lethal raids), and the attackers significantly outnumbered their victims (median 8:1 ratio: Wilson et al., 2014). A few males killed unrelated unweaned infants (Wilson et al., 2014), known as infanticide, a male reproductive strategy among male-dominated groups. Infanticide allows the male to impregnate the victim's mother quicker than if he waits for the female to complete lactation (Lukas & Huchard, 2014). Furthermore, there is considerable variation in aggression among chimpanzee subspecies. For example, western chimpanzees (*P. troglodytes verus*), have lower rates of aggression (Boesch et al., 2008; Wilson et al., 2014; Wrangham, 1999) because they face different ecological and social pressures (Wittiger & Boesch, 2012).

However, in addition to aggression, peacekeeping is also a vital component of these social animals' behavioral repertoire (de Waal, 2007). When intragroup aggression occurs, males engage in reconciliatory behavior by maintaining eye contact, embracing, and kissing to mend their relationships (de Waal, 2005). So, while males certainly are more aggressive than females, these reconciliations are crucial to preserve cooperative relations within their coalitions (de Waal, 2005). Male-male bonding plays a remarkable role in strengthening their coalitions (Stevens et al., 2006). Their male-male kinship bond shapes their fluid and peaceful groupings (Strum & Fedigan, 2000). While aggressive behaviors persist due the adaptive benefits aggressors might gain, reconciliation behavior is also needed to maintain peace in their social bonds that influence overall rank (Wilson et al., 2014).

While males typically exhibit more aggressive behavior towards each other when competing for access to fertile females (Trivers, 1972), female-female competition occurs when an immigrant female jeopardizes an established female's access to high-quality foraging territory

(Kahlenberg, Emery Thompson, & Wrangham, 2008). Because high rank is positively correlated to high-quality foraging areas, resident females aggressively target immigrants who pose a threat to the established rank and their subsequent reproductive success (Kahlenberg, Thompson, & Wrangham, 2008; Pusey & Schroepfer-Walker, 2013). Furthermore, when females are in estrus, they are more likely to avoid one another in competition for limited food resources, as opposed to anestrus females who are more gregarious, or affiliative (Pepper, Mitani, & Watts, 1999). Within fission-fusion societies, in which size and composition of the social group changes over time due to food availability, females generally forage alone or in small subgroups to avoid direct competition (Pusey & Schroepfer-Walker, 2013).

In comparison to males' frequent changes in rank, rank challenges among females are rare. Unlike competing males, females are less likely to benefit from escalated aggression (Foerster et al., 2016). Rank is relatively static and maintained by long-term dominance relationships (Foerster et al., 2016). Females thus "queue," or line up, for social status and rely on alliances to support their relative rank (Foerster et al., 2016). If a natal female forgoes immigration, she holds a higher rank while her mother is still alive compared to immigrant females and natal females whose mother has died and holds lower rank (Foerster et al., 2016). Because rank is fixed and tenure based, it is important for immigrating females to enter rank as high as possible to gain access to high quality foraging territories (Foerster et al., 2016; Pusey, Williams, & Goodall, 1997).

Most mammalian males control reproduction (Klinkova et al., 2005), including chimpanzees (Roberts & Bradley Roberts, 2015), making the female's offspring subject to infanticide (Lukas & Huchard, 2014). As previously mentioned, infanticide is a reproductive strategy by which males target and kill unrelated infants. This makes the female stop lactating

and come into estrus, allowing the male to impregnate the victim's mother more quickly than if he had waited for her to wean her infant (Lukas & Huchard, 2014). By killing an infant, infanticide reduces the female's reproductive fitness but increases the dominant male's reproductive fitness.

Among chimpanzees, however, infanticide occurs at relatively low rates (Boesch et al., 2008; Murray, Wroblewski, & Pusey, 2007; Wilson et al., 2014). To counteract male infanticide, females have evolved to mate with multiple males to confuse paternity (Lukas & Huchard, 2014; Watts, 2007). However, males still compete for fertile females through sperm competition (Parker, 1970; Wroblewski et al., 2009). While the female continues to mate with multiple males, male sperm competition ensures that quality sperm penetrates the egg. Alternatively, to ensure paternity some males engage in aggressive mate guarding toward females. Others will go on consorts, another form of mate guarding whereby males travel with females outside of their territory to prevent fertile females from mating with other males (Watts, 2007). So, while males may generally be more gregarious than non-fertile females, they are not more gregarious than females in estrus (Pepper, Mitani, & Watts, 1999).

Unlike other chimpanzee groups, but like their female-dominant cousins, bonobos (*Pan paniscus*), female western chimpanzees from the Tai community in Ivory Coast occasionally form coalitions to counteract male aggression (Newton-Fisher, 2006). Notably, these females are more gregarious than other females in wild populations (Newton-Fisher, 2006; Wittiger & Boesch, 2013).

Particularly, in the Tai community, female gregariousness increases with greater numbers of female in estrus and clumped fruit (Wittiger & Boesch, 2013). Moreover, when fruit is scarce, females with higher rank are more gregarious than females with lower rank (Riedel, Franz, &

Boesch, 2011). Despite foraging territories that overlap by around 85% and the expectation of competition for food, female party size increases with increasing numbers of females in estrus (Wittiger & Boesch, 2013). Compared to female eastern chimpanzees (*P. troglodytes schweinfurthii*) who typically avoid one another (Pepper, Mitani, & Watts, 1999), female western chimpanzees prioritize their female friendships when fruit is abundant. Therefore, the differences observed between chimpanzees and bonobos, as well as humans, may be more of degree rather than kind (Newton-Fisher, 2006) and are highly dependent on access to food resources.

Another influence on group relationships is sociosexual behavior. Sociosexual behavior includes any form of non-conceptive genital contact both within and between sexes (Sandel & Reddy, 2021). In great apes, sociosexual behavior reduces tension and prevents conflict (Hohmann, Mundry, & Deschner, 2009; de Waal, 1987). In the first study on male chimpanzee same-sex sociosexual behavior, Sandel and Reddy (2021) found that this behavior stimulates and assists the formation of male's cooperative coalitions. Sociosexual behavior plays a vital role in social interactions by reducing tension between unfamiliar individuals and providing reassurance to a nervous individual following conflict (Macfarlane & Vasey, 2016; Sandel & Reddy, 2021).

Same-sex sexual behavior is observed in several non-human animal taxa, including mammals, birds, reptiles, amphibians, insects, mollusks, and nematodes through same-sex courtship, pair bonding, and copulation (Bailey & Zuk, 2009). However, data collection on this behavior has largely been disregarded due to the assumption that individuals engaging in these sexual acts are of the opposite sex (Bailey & Zuk, 2009). From an evolutionary perspective, same-sex sexual behavior seems unusual because there is no direct result in reproduction. This long-established perspective not only invalidates the heterogeneity of human sexuality, but it also negates scientific discovery.

Until recently, researchers dismissed same-sex sociosexual behavior in chimpanzees as an act of reassurance (Sandel & Reddy, 2021). However, Sandel & Reddy (2021)'s study at Ngogo, in Kibale National Park, Uganda found that sociosexual behavior is unrelated to dominance. Sociosexual behavior occurred in all age and sex classes, especially among adolescent and young adult males. The same-sociosexual behavior and group hunts occur at similar rates (Sandel & Reddy, 2021). Thus, sociosexual behavior is a significant aspect of chimpanzee social life.

In general, males at Ngogo have higher rates of cooperative behavior, group hunts, and border patrols than other chimpanzee populations (Langergraber et al., 2007; Mitani, 2009; Mitani & Watts, 2001). Some individuals may seek and engage in more sociosexual behaviors, which does not necessarily speak to sexual orientation (as it might do in humans), but to the individual seeking reassurance (Sandel & Reddy, 2021). More so, the frequency of sociosexual behavior may be underrepresented because the behavior happens quickly, especially for individuals who seek reassurance following aggressive events (Sandel & Reddy, 2021). Furthermore, there is a lack of evidence on same-sex sexual behavior in the historical literature probably because of cultural biases against homosexuality (Vasey, 1995). But overall, Sandel and Reddy (2021) conclude that sociosexual behavior is common in haplorrhine primates.

Though there has been a lack of explicit reports of chimpanzee sociosexual behavior, that does not mean that it is a newly identified phenomenon in great apes (Klinkova et al., 2005; Sandel & Reddy, 2021; Wallis, 1992). Bonobos, the chimpanzee's cousin, have high rates of sociosexual behavior, especially between females (Furuichi, 1989; Idani, 1991; Moscovice et al., 2017, 2019; Ryu, Hill, & Furuichi, 2015; Tokuyama & Furuichi, 2016; Wrangham & Peterson,

1996; de Waal, 1995). Female bonobos, like male chimpanzees, form coalitions. Same-sex sociosexual behavior has critical influence on cooperative coalition formation.

Similarly, within both chimpanzee and bonobo coalitions, individuals who are the dominant sex frequently exhibit same-sex sociosexual behavior. As I discuss in the next chapter, sociosexual behavior, is more frequent in bonobos than chimpanzees (Sandel & Reddy, 2021). However, the findings of sociosexual behavior in chimpanzee coalitions conveys its importance in forming bonds within the community. Researchers in the past might have chosen to ignore naturally occurring same-sex sociosexual behavior out of fear of condoning homosexuality. However, this fear ignorantly negates scientific discovery.

All aspects of sexual behavior must be studied to understand sociosexual behavior's function and its social benefits and its function in all animals. Regardless of commentaries about human nature, bonobos, whose society is marked by same-sex sociosexual behavior (Furuichi, 1989; Idani, 1991; Moscovice et al., 2017, 2019; Ryu, Hill, & Furuichi, 2015; Tokuyama & Furuichi, 2016; Wrangham & Peterson, 1996), reveals the crucial need to study diverse evolutionary trajectories from a broader perspective. Chimpanzees inform us about our own species, but one must be cautious of its potential to sustain male-dominated oppression in human patriarchal societies. In other words, a three-way comparison between humans, chimpanzees, and bonobos is crucial to understand human social origins (de Waal, 2006) and propose more equitable futures for Western cultures.

CHAPTER III: Bonobos: Understanding female-dominance

“Female power is a sine qua non of bonobo life, the magic key to their world” (Wrangham & Peterson, 1996, p. 221).

Bonobos (*Pan paniscus*) are female-dominant and form fission-fusion groups with promiscuous mating patterns. They maintain female social dominance via unrelated female coalitions (Moscovice et al., 2019). There is controversy as to whether bonobos are female-dominant (Parish, 1996; Parish & de Waal, 2000), codominant between sexes (Kano, 1996; Kuroda, 1980), matrifocal (mother or female centered: Furuichi, 1997), or nonexclusive female-dominant (Vervaecke, de Vries, & Van Elsacker, 2000a). Because females generally occupy higher ranks than males (Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016) and influence mating and relationships patterns among group members (Surbeck et al., 2019), I define bonobos as female dominant. However, there are nuances within the hierarchy in which some males with high-ranking mothers are dominant over other females (Stevens et al., 2007). Overall, bonobo’s female bonds and their affiliative coalitions are principal characteristics of their species and set them apart from other primates (Moscovice et al., 2017; Tokuyama & Furuichi, 2016).

Often, as I described in the previous chapter, same-sex sexual behavior facilitates coalition formation (Moscovice et al., 2019). Female coalitions are typical in primates with female philopatry, in which males disperse at sexual maturity and females remain in their natal group and form coalitions with their kin (Tokuyama & Furuichi, 2016). While direct fitness is the number of offspring an individual produces, and indirect fitness is the number of their relatives’ offspring weighted by degree of relatedness, inclusive fitness is the sum of direct fitness and indirect fitness (Hamilton, 1964). Within coalitions of related females, cooperative

and altruistic behaviors increase overall inclusive fitness. When related females form coalitions, kin selection theory suggests they are more inclined toward cooperative and altruistic behavior to maximize their inclusive fitness offspring (Eberhard, 1975; Quellar, 1992).

However, bonobos are male-philopatric (Tokuyama & Furuichi, 2016). Females leave their birth groups upon sexual maturity and are thus unrelated. Therefore, kin selection theory alone cannot explain why unrelated females form coalitions. Theoretically, because bonobos can rely on multiple food resources, like fruits and herbs (Wrangham & Peterson, 1996), females, whose reproductive success is limited by access to food resources in mammals (Trivers, 1972), are not in severe reproductive competition.

The abundance of sexual behavior likely evolved due to abundance of resources. And while frequent sociosexual behavior aids in forming such cohesive societies, bonobos had the flexibility to do this because of the “low cost-of-grouping” (Wrangham & Peterson, 1996) associated with reduced competition for resources, particularly among females. The common ancestor of the bonobo and chimpanzee lived around 1.7 million years ago (Kovalaskas, Rilling, & Lindo, 2021). The two species diverged because of the ecological barrier formed by the Zaïre (Congo) River (Wrangham & Peterson, 1996). The ecosystems on either side of the river are almost entirely identical, composed of the same tree species, forest structure, and foods. The main differences between the two species are their diets and the other species with which they share an ecosystem.

Chimpanzees mostly consume fruits, but bonobos eat both fruits and fibrous foods (Malenky, 1994). Moreover, chimpanzees and gorillas are sympatric species (Wrangham & Peterson, 1996), meaning that by living in near proximity, these two species compete for food resources. In their sympatric environment, gorillas consume the fibrous foods that bonobos eat

south of the Zaire River. During seasonal fruit shortages, while chimpanzees compete over limited food resources, bonobos rely on abundant fibrous foods to travel in larger cohesive groups (Wrangham & Peterson, 1996). Ultimately, their ability to digest hard-to-process abundant foods supports their flexible group behavior: they can promote affiliative social behavior rather than defer to contest competition for resources. Therefore, in the context of their evolution, “food played a larger role than sex” (Haraway, 1984, p. 513). Adding new group members does not impact the food supply; new group members only offer positive affiliative relationships. In this aspect, strong female affiliative relationships deter male aggression which could otherwise theoretically enable male’s control of female sexuality. Notably, bonobo societies differ from chimpanzee societies who rely on their abundance of food resources to substitute sex for aggression (de Waal, 1995).

Without resource competition, female coalitions were able to evolve as a counterstrategy against male harassment (Tokuyama & Furuichi, 2016). Following harassment, females direct coalitionary reactive aggression against unrelated, lower-ranking males (Vervafcke, de Vries, & van Elsacker, 2000b). While they are aggressive, these coalesced females never enact lethal aggression (Wilson et al., 2014). Furthermore, coalition formation within bonobo groups is exclusive to females (Wrangham & Peterson, 1996). Same-sex sociosexual behavior among females facilitates and strengthens social bonds to ultimately avert male aggression.

Close spatial proximity, grooming, and genito-genital rubbing (GG-rubbing, in which two females rub their genitals together) assist and strengthen bonds within their female coalitions. In one study, sexual interactions composed 65% of recorded behavior in unrelated female dyads (Moscovice et al., 2019). Of these interactions, more than 98% involved GG-rubbing (Moscovice et al., 2019). In the context of feeding, GG-rubbing female same-sex sexual

interactions are more frequent than intersexual sexual interactions (Moscovice et al., 2019). A significant increase in female oxytocin levels succeeding female sexual interactions suggests same-sex sociosexual behavior facilitates cooperation among female coalitions to avert male harassment while feeding (Moscovice et al., 2019; Tokuyama & Furuichi, 2016).

And while both males and females engage in same-sex sociosexual behavior, the rates are significantly higher among females (de Waal, 1995). The low rate of male intrasexual interactions explain low levels of cooperation and heightened aggression among males (Moscovice et al., 2019; Tokuyama, Sakamki, & Furuichi, 2019). When interacting with females outside of their group, females continue to rely on same-sex sexual behavior to promote cooperation (Tokuyama, Sakamki, & Furuichi, 2019). Males, however, are more aggressive toward intergroup males (Tokuyama, Sakamki, & Furuichi, 2019).

Not only do female same-sex sexual interactions promote cooperation (Moscovice et al., 2019), it is possible that females are simply attracted to other females. Adolescent females immigrate into groups and form bonds based on experience, not kinship (Wrangham & Peterson, 1996). Females must work to develop these important bonds that strengthen cooperation against male aggression (Wrangham & Peterson, 1996). For example, reports indicate that once an adolescent female enters a new group, she targets an older female with whom to develop a social bond (Idani, 1991; Furuichi, 1989; Wrangham & Peterson, 1996; Tokuyama & Furuichi, 2016). The subordinate adolescent female remains near and shows interest in the older female, but it is only when the older female initiates the social interaction does the adolescent female reciprocate. Subsequently, their social bond is reinforced by same-sex sociosexual behavior.

Wrangham & Peterson (1996) describe these female-female interactions as a sort of “falling in love” (p. 209). We cannot know if these animals are truly “falling in love” but

certainly their social interactions can be compared to what falling in love looks like in humans: sitting closely to one another, alertness to reciprocal glances, reciprocal grooming, and sexual interactions. Once thereafter the females engage in GG-rubbing, their social bond is significantly strengthened (Wrangham & Peterson, 1996). Furthermore, within this female friendship and sexual relationship, dominant females respect their subordinates, and the immigrant female successfully enters a network of support and security (Wrangham & Peterson, 1996).

Female friendships and sexual relationships are positively selected for to promote ease of immigration. Female bonobos have significant periods of prolonged sexual swellings in relation to the estrus cycle, characterized by exaggerated swelling and coloration of the perineum skin (Ryu, Hill, & Furuichi, 2015). Data support that prolonged maximal swellings promote female affiliative bonds and attractiveness to one another (Ryu, Hill, & Furuichi, 2015). Swellings last well beyond the ovulation period (Reichert et al., 2002), with maximal swellings that can last for more than 20 days (Furuichi, 1987).

Not only do females with maximal sexual swellings engage in copulation and GG-rubbing more frequently than females without sexual swelling, but they also engage in reciprocal grooming more often (Ryu, Hill, & Furuichi, 2015). Therefore, the prolonged sexual swelling may be a physiological adaptation that functions to increase affiliative behavior within female coalitions (Ryu, Hill, & Furuichi, 2015). This finding is congruent with an increase in oxytocin levels following GG-rubbing between females (Moscovice et al., 2019). While sexual swellings initially evolved as a sexual signal to males, prolonged sexual swellings now also function to attract females (Ryu, Hill, Furuichi, 2015). These prolonged sexual swellings are especially important for young immigrant females who rely on sociosexual behavior to promote ease of

entering a new group (Ryu, Hill, & Furuichi, 2015). Thus, bonobo sex has evolved to facilitate and maintain female friendships.

While female bonding and sociosexual behavior is initially high for immigrant females (Ryu, Hill, & Furuichi, 2015), relations with females weaken as the bond with their offspring takes precedence (Furuichi, 1989). Once coalitionary groups are stabilized, female-female bonding declines (Stevens et al., 2006). Grooming is most common among the mother-son dyad (Stevens et al., 2006). And while female-female bonds certainly support and strengthen their coalitions (Moscovice et al., 2019), mothers encourage their sons to befriend unrelated adult females (Stevens et al., 2006). Female same-sex and immature-adult intersexual sexual interactions are more frequent than adult intersexual sexual interactions, (Manson, Perry, & Parish, 1997). With strong mother-son bonds, mothers act as matchmakers to facilitate immature-adult intersexual relationships (Surbeck et al., 2019).

Affiliative bonds between mothers and sons increase paternity success (Surbeck et al., 2019). To increase their mating success, mothers often bring their sons into close spatial proximity to estrus females, restrict other males from interfering with her son's mating, interfere with unrelated males' mating (Surbeck, Mundry, & Hohmann, 2011), and form coalitions with their sons so that they maintain a high dominance rank (Furuichi, 2011). Mothers encourage their sons to befriend unrelated females. Because mothers increase paternity success by facilitating unrelated male-female social bonds (Surbeck et al., 2019), and due to the general trend that females are dominant over males (Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016), it pays off for immature males to befriend unrelated adult females (Furuichi, 1997; Hohmann et al., 1999). Therefore, affiliative male-female bonds evolved because of strong mother-son bonds (Hohmann et al., 1999). As a mother who helps avert male aggression within her coalition, she

encourages her son to be kind to unrelated females. The existence of male-female friendships suggests platonic intersexual relationships reduce intersexual conflict. Thus, not only have female friendships reduced overall aggression in bonobos (Wilson et al., 2014), but they have also selected for kinder males.

High rates of affiliation among males and females and frequent sociosexual behavior distinguishes bonobos from other apes (de Waal, 1995). Bonobo females, with their high affinity to share and selection for kinder males, facilitate fair practices. Bonobos, while they are female-dominant, are equitable. Rather than provide males and females equal feeding opportunities, female bonobos first establish peace (via sociosexual behavior) and ensure females, whose reproductive success is limited by access to food (Trivers, 1972), have priority access to food (White & Wood, 2007). By maintaining fair practices in their platonic and mating relationships, bonobo female-dominance promotes equity. Like bonobos, human females also rely on female friendships for support (Reynolds, 2021). However, humans also form pair-bonds with their sexual partners (Fernandez-Duque, Valeggia, & Mendoza, 2009). Therefore, it is crucial to analyze egalitarian pair-bonds, as observed in gibbons and siamangs (Hylobatidae), who foster equality in shared parental care (Fernandez-Duque, Valeggia, & Mendoza, 2009).

CHAPTER IV: Gibbons and siamangs: Understanding egalitarianism

“‘Monogamous’ gibbons really swing” (Gibbons, 1998).

The lesser apes, gibbons (genera *Hylobates*, *Hoolock*, and *Nomascus*) and siamangs (genus *Symphalangus*), make up the family Hylobatidae. Humans and gibbons share a common ancestor that lived twenty to sixteen million years ago (Kenyon et al., 2011). Today their geographic distribution ranges from northeast India to west Bangladesh to southern China and Indonesia (Kenyon et al., 2011). Most gibbons are socially monogamous and form a pair bond between an adult male and female. Within the pair-bond, they lack an explicit dominance hierarchy (Kleiman, 1977). The pair typically live in nuclear family units with 2-6 members, including their dependent offspring (Reichard, 1995).

Both sexes disperse only after reaching sexual maturity (at around 8 years of age: Hu et al., 2018). In animals living in nuclear-family groups it may be costly to disperse before reaching sexual maturity because it pays off to receive prolonged familial support (Wittenberger & Tilson, 1980). Many gibbons and siamangs therefore delay dispersal from their natal territory by about two years and disperse at around 7 to 10 years (Brockelman et al., 1998; Reichard, Ganpanakngan, & Barelli, 2012). Sub-adults may delay dispersal even longer to promote inclusive fitness (Brockelman et al., 1998; Emlen, 1995).

Typically, in a monogamous social system, pairs mate exclusively with one another (Fuentes, 1998). Monogamous pairs share parental care (Emlen & Oring, 1977). Neither sex can monopolize sexual reproduction (Emlen & Oring, 1977). Most gibbons and siamangs are socially monogamous, but there are a few cases of polygyny (*Nomascus concolor*: Haimoff et al., 1986; Bleisch & Chen, 1991; Jiang et al. 1999) and polyandry (*Symphalangus syndactylus*: Lappan, 2007; *Hylobates lar*: Barelli et al., 2008). And while they are socially monogamous, they are

sexually promiscuous with significant rates of cheating (extra-pair copulation, or EPC: Kenyon et al., 2011; Lappan, 2007; Leighton, 2008; Palombit, 1994a; Palombit, 1994b; Reichard, 1995; Reichard, 2005; Reichard, 2009; Savini, Boesch, & Reichard, 2009).

The strength of the pair-bond is taxon specific. A study on three species of Hylobatidae (siamangs [*Symphalangus syndactylus*], crested gibbons [*Nomascus*], and pileated gibbons [*Hylobates pileatus*]) found varying degrees of pair-bond strength, with siamangs exhibiting the strongest pair-bond and pileated gibbons a weaker relative pair-bond (Geissmann et al., 2020). This could be because male siamangs invest more direct paternal care and are thus more invested in the partnership (Geissmann et al., 2020; Lappan, 2005). Additionally, there are higher rates of polygyny among the genus *Nomascus*, which may be attributed to its varied strength of the pair-bond (Geissmann et al., 2020). In these polygynous social groups, females groomed each other, shared meat, and formed coalitions to evict a dispersing female trying to join their group (Hu et al., 2018).

Polygynous females may be more cooperative than monogamous pairs because females, to maximize their reproductive output, will exclude outside females who attempt to displace one of them (Hu et al., 2018). These females, who rely more on males to defend the territory and resources rather than direct paternal care (Kleimann, 1977), are thus influenced by different ecological factors, such as range size, patch size, patch distribution, and reduced costs of predator detection and evasion (Kappeler & van Schaik, 2002) as compared to other gibbons who live in pairs. However, pair-bonded gibbons and siamangs ultimately adapt to the specific social relationship. For example, a study I helped conduct at Denver Zoo found that same-species pairs (*Symphalangus syndactylus*) and mixed-species pairs (male *Nomascus gabrielle*, female *S. syndactylus*) have similar activity budgets and remain in close spatial proximity to one another

(Figure 1, Figure 2). Despite taxon specific pair-bonded strength, ultimately, an individual's welfare is maintained when she is housed with a related species. Therefore, the individual is flexible in forming pair-bonds.

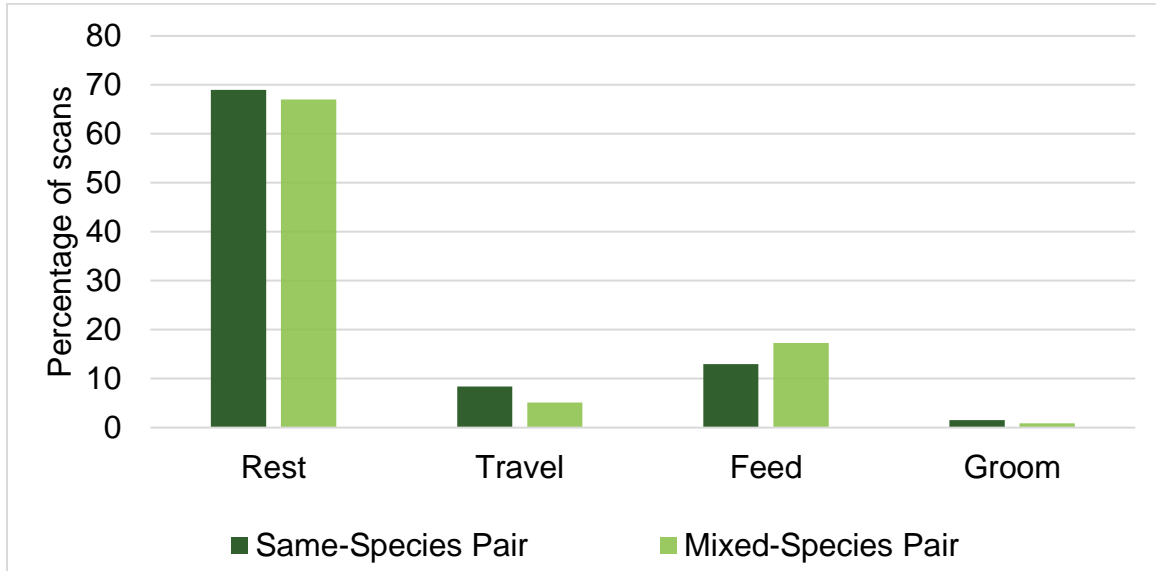


Figure 1: Activity budgets of captive same-species pair (dark green bar: *S. syndactylus*) and mixed-species pair (light green bar: male *N. gabrielle*, female *S. syndactylus*) at Denver Zoo, Denver, CO. While there were no significant differences across pairs in time spent resting, locomoting, and feeding, the same-species pair spent significantly more time grooming (1.5%) than the mixed-species pair (0.95%; $p = 0.007$).

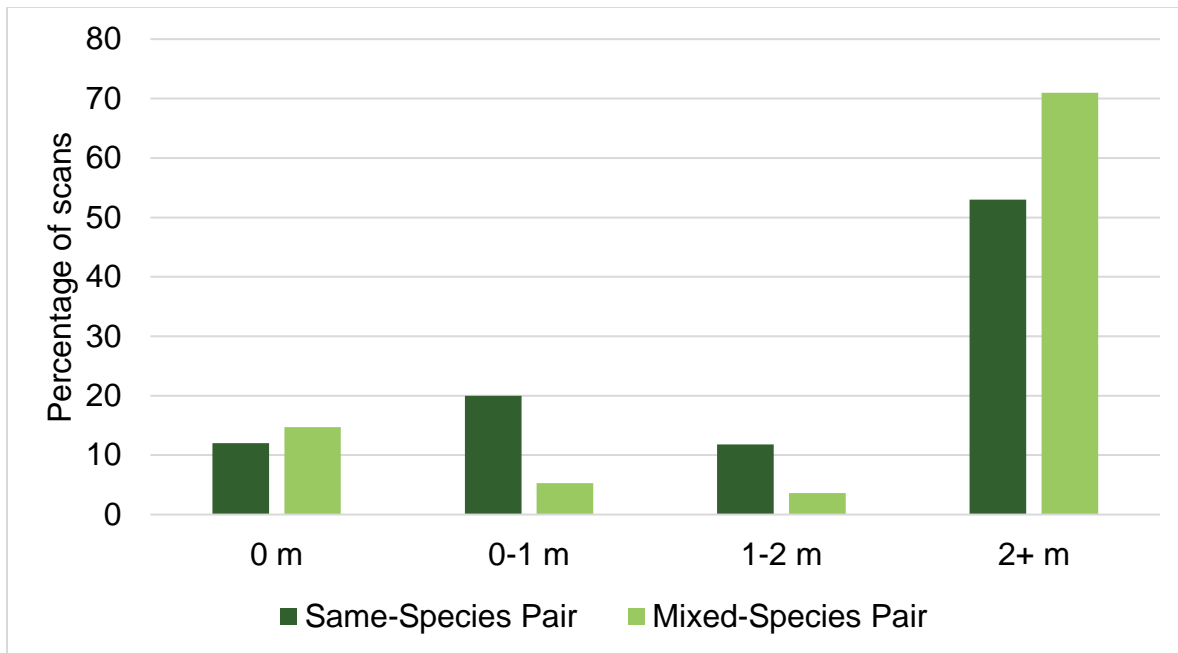


Figure 2: Spatial proximity of captive same-species pair (dark green bar: *S. syndactylus*) and mixed-species pair (light green bar: male *N. gabrielle*, female *S. syndactylus*) at Denver Zoo, Denver, CO. Both pairs spent equal amounts of time in physical contact, although the mixed-species pair spent significantly more time farther than 2 m apart (mixed-species pair=71%; same-species pair=53%; $p=0.006$).

Social monogamy evolved as a reproductive strategy to reduce the likelihood of infanticide and control for paternal certainty (Palombit, 1999). Species with long interbirth intervals (for gibbons approximately 2-5 years: Palombit, 1995), long lactation relative to gestation, and infant carrying by the mother, like gibbons as well as siamangs (at least until the child is weaned, then males carry the offspring: Lappan, 2008), have high risk for infanticide (van Schaik, 2000). However, the significant rates of “cheating” (Palombit, 1994b; Reichard, 1995) and “divorce,” whereby young adult males might abandon their original mate to join a female and her offspring who are unrelated to the male, or a young unmated male might replace a partner after the death of a mate (Palombit, 1994a), reduce paternal certainty.

Among pair-living species, EPC is frequent (Reichard, 2005). EPC is a female reproductive strategy to mate with males who offer “good genes” and remain with their pair-bonded male mate who provides high quality paternal care (Reichard, 1995). So, while gibbons are socially monogamous, female choice has crucial influence on their flexible reproductive behavior (Reichard, 1995). The female thus has considerable choice to optimize her own reproductive success. Furthermore, in gibbon and siamang’s egalitarian pair-bond, neither sex can monopolize reproduction when females and males cheat.

Gibbons and siamangs have relatively low rates of aggression (Amarasinghe & Amarasinghe, 2011; Lappan, 2007). In a study on gibbons, pair-mates sometimes use aggression to break up EPC attempts (Palombit 1992, 1994b), but successful EPCs usually occur at a far distance from the pair-mate (>20m: Palombit, 1992). However, in another study on siamangs, EPC are successful at a short distance (<20m) from the pair-mate when they are likely aware of the EPC (Lappan, 2007). Thus, the degree of monogamy and indifference toward EPC is likely dependent on the individual or is taxon-specific. Despite this cheating, shared parental care, either through direct or corresponding patterns of paternal care, remains a crucial element in their socially monogamous relationship (Fernandez-Duque, Valeggia, & Mendoza, 2009).

Furthermore, at least in Western societies, monogamy is associated with egalitarianism – equality between the sexes (Kanazawa & Still, 1999) – because parental duties are distributed in the pair-bond. Generally, among mammals, females demonstrate more parental care than males (Trivers, 1972). Male gibbons, however, only show correlates of paternal care, such as social monogamy, territoriality, and reduced sexual dimorphism (Fernandez-Duque, Valeggia, & Mendoza, 2009), as opposed to direct paternal care, which includes carrying infants. Male

siamangs, on the other hand, do provide direct paternal care and carry the infant one year after birth (Cunningham & Mootnick, 2009; Lappan, 2008; Rafacz, Margulis, & Santymire, 2012).

Direct paternal care evolves because of obligate biparental care, whereby both parents are needed to promote the survival of the offspring (Achenbach & Snowdon, 2002; Fite et al., 2005; Miller et al., 2006; Smucny et al., 2004; Tardif et al., 2005; Van Schaik & Kappeler, 1997). In siamangs, males carry and care for infants following weaning until they are fully independent (Cunningham & Mootnick, 2009). Siamangs, who reach sexual maturity at a later age than most other gibbons (8 to 9 years versus 6 to 8 years: Geissmann, 1991), may require this greater degree of direct paternal care to successfully raise their offspring to maturity (Kleimann, 1977).

When male and female siamangs both carry the offspring, the offspring doesn't receive *more* overall parental care, but rather the male siamang *reduces* the energetic costs associated with the female carrying the unweaned infant (Lappan, 2007; 2008). Furthermore, the male alleviates some of the female's reproductive costs. Consequently, when males aid in paternal care, females' interbirth interval (IBI) decreases, but when males reduce their paternal care, females carry the offspring for longer and her IBI increases, and thus lowers her overall potential fitness (Lappan, 2008). Paternal care among siamangs reduces energetic costs for females, allowing females to reach higher reproductive rates with lower interbirth intervals (Lappan, 2005; 2008).

Even though both males and females cheat on their pair-mate (Kenyon et al., 2011; Lappan, 2007; Leighton, 2008; Palombit, 1994a; Palombit, 1994b; Reichard, 1995; Reichard, 2005; Reichard, 2009; Savini, Boesch, & Reichard, 2009), shared parental care is a vital component to the survival of gibbon and siamang offspring (Fernandez-Duque, Valeggia, & Mendoza, 2009). The pair-bond is characterized as the core unit of gibbon and siamang social

life (Kleiman, 1977; Reichard, 1995). Female choice leads to the significant rates of EPC, allowing the mother to weigh the benefits and costs of cheating to simultaneously obtain “good” genes and shared parental care.

However, within their egalitarian grouping, female choice only goes so far. Besides the events of EPC, male and female Hylobatidae only interact with their pair-bonded mate and defend their territory with vocal displays to fend off intruders (Reichard & Sommer, 1997). Unlike chimpanzees, bonobos, and humans, who form fission-fusion societies and interact frequently with other individuals within the group (Aureli et al., 2008), gibbons and siamangs, with reduced aggression compared to other apes, including humans (Amarasinghe & Amarasinghe, 2011; Lappan, 2007), typically affiliate only with familiar family members (Liebal, Pika, & Tomasello, 2004). Despite the importance of female choice and paternal care in gibbon and siamang society, egalitarianism does not promote equity in Western society because women should be treated fairly both within and outside of their sexual relationships. Ultimately, Western women need equity in all their social relationships.

CHAPTER V: Intersecting primatology and feminist theory

“The master’s tools will never dismantle the master’s house” (Lorde, 2003).

Patriarchy manifests through rigid gender roles (Becker, 1999) and preserves androcentric social and political systems (Lerner, 1986). While patriarchy persists in Western cultures, there are numerous egalitarian and matrilineal societies that exist outside of the West (Graeber & Wengrow, 2021; He et al., 2016; Robinson & Gottlieb, 2021). Patriarchy persists insofar as men maintain power over women. Moreover, women and men who challenge gender roles destabilize patriarchy (Becker, 1999).

Nonhuman primates, however, highlight that female choice is central to primate social systems. Because females are the limiting sex in mammals, meaning that to reproduce, females incur significant energetic costs to produce an egg and carry offspring (Trivers, 1972), female choice has a cascading effect on primate group’s social organization. If female choice is central to primate life, why has women’s choice been diminished in modern patriarchal human history? By comparing the role of nonhuman female primates in male-dominated, female-dominated, and egalitarian social systems, Westerners ought to distribute more power to women to rightfully highlight the essential role they play in our human primate social system.

Throughout history, there have been numerous strides toward demanding gender equality in Western society, like citizenship, voting rights, property rights, and reproductive justice, to amend women’s systemic oppression (Launius & Hassel, 2018). While women are now legally able to hold positions of power, male power is preserved by patriarchal institutions. Women are required to navigate political and economic systems that uphold male power. Even though Western society has reached somewhat a state of equality by offering the same opportunities to men and women, social and political systems often fall short in delivering equal outcomes

because of historic and systemic male privileges conserved by patriarchy. Equity, on the other hand, ensures that fair opportunities effect equal outcomes to rectify systemic injustices (Cook & Hegtvedt, 1983). In Western society, there will only be true gender equality when gender equity is first established.

In general, feminism strives to combat and critique patriarchy (Launius & Hassel, 2018). According to feminist and social activist bell hooks,

Feminism is a struggle to end sexist oppression. Therefore, it is necessarily a struggle to eradicate the ideology of domination that permeates Western culture on various levels, as well as a commitment to reorganizing society so that the self-development of people can take precedence over imperialism, economic expansion, and material desires (26).

To reach a state of gender equity, every man and woman must work against misogynistic institutions that perpetuate sexist oppression. Furthermore, when feminism embodies all members of society – including men – it has the potential to improve the lives of all people and promote human flourishing (Becker, 1999). So, to reduce the gender gap of relative inequality, feminists must disassemble and reconstruct Western social gender norms that have historically aggrandized male power yet discouraged female power.

Certainly, compared to Western culture, gender roles vary in egalitarian and matrilineal societies. However, in egalitarian and matrilineal (descent from the maternal line) societies, primarily hunter-gatherers (Graeber & Wengrow, 2021; Lee, 1974) and subsistence farmers (He et al., 2016; Mattison et al., 2018), respectively, have completely different structures and customs. While I do argue that power in Western society must be radically redistributed, reverting to hunter-gatherer and subsistence farming practices is near impossible in the persistent Western capitalistic society (Graeber & Wengrow, 2021). The presence of human egalitarian and

matrilineal societies alone, however, support that the West can in fact change the way they organize gender roles. And to obtain gender equity, Western civilization must first grant more power to women.

Many men may be reluctant to help fight for gender equity because of hegemonic masculinity. Hegemonic masculinity is a culturally defined set of masculine traits. Western culture defines masculinity as being unemotional, independent, non-nurturing, aggressive, and dispassionate (Connell & Messerschmidt, 2005). Hegemonic masculinity forces individuals to conform to certain gender identities: men will be assertive and dominant while women will be coy and submissive. Hegemonic masculinity encourages men to actively represses feminine characteristics (Becker, 1999), thus depriving them of their full personal and emotional capacities as humans. Western patriarchy ultimately sustains toxic hegemony. Hegemonic masculinity requires that men be dominant, unemotional leaders (Connell & Messerschmidt, 2005). Because of this, hegemonic masculinity promotes that society reject folks who challenge the rigid gender binary. Men thus may be resistant to challenge patriarchal gender norms. However, to end the sexist of oppression of all people in society, the West must deconstruct masculine and feminine attributes that are attached to certain genders, through the concept of relational feminism (Becker, 1999).

Relational feminism does not reject formal equality and dominance feminism, but rather seeks fulfillment for women and men and seeks to treat people similarly regardless of their gender (Becker, 1999). To effect systemic change, Westerners must reconstruct legislative bodies that truly reflect the diverse perspectives of those who have been underrepresented, including but not limited to, women, racial and ethnic minorities, queers, and working- and lower-class peoples (Becker, 1999). Today, with substantial improvements to political

representation, many women in leadership positions no longer need to display traditionally “masculine” characteristics, and many men are encouraged to embrace their emotional identity that hegemonic masculinity suppresses. Only when diverse perspectives are shared and heard can the West actively deconstruct preestablished gender roles.

Non-Western societies successfully distribute power across women and men. Compared to patrilineal societies (descent from the paternal line), matrilineal societies encourage active female participation in economic and political spheres (Robinson & Gottlieb, 2021). The Bantu Matrilineal Belt in sub-Saharan Africa, for example, demonstrates exceptional female political participation (Robinson & Gottlieb, 2021). Since women in matrilineal societies have greater access to social and material resources, they subsequently have greater access to education (Robinson & Gottlieb, 2021). An individual’s decision to participate in economic and political spheres is influenced by money and knowledge they possess (Verba & Nie, 1987).

When society organizes to offer the maternal line access to material and social resources, most everyone expects that women should have equal access to these resources (Robinson & Gottlieb, 2021). In other words, when a culture sets the precedent for gender equality, their people respect that standard. The long-term institution of matrilineality positively impacts gender equality and female political participation. Laws that are passed to provide women with access to resources, such as money and education, offer short-term interventions (Robinson & Gottlieb, 2021). However, the long-term structural institution of matrilineality is more successful at bridging the gender gap. Therefore, in the West, where political systems tolerate gender inequality by preserving patriarchal institutions, short-term legal intervention will not secure gender equity. Alternatively, the West must grant more political power to women who can represent themselves and reform systems that structurally oppress marginalized groups.

It is time for Western political power to be redistributed to women. Male domination has persisted for 10,000 years too long (Hrdy, 1997; Reynolds, 2021). Human evolution has, by and large, been studied through the lens of the male-dominant chimpanzee (*Pan troglodytes*), one of humanity's closest living relatives. Therefore, many people assume that male-dominance in humans coincides with aggression (Wrangham & Peterson, 1996). However, it is equally important to recognize that our other closest living relative, the bonobo (*Pan paniscus*), diverged down an evolutionary path devoid of male-dominance. When evolutionary models strictly compare human and chimpanzee social systems, ordinary people (i.e., people who are not sociobiologists) remain under the delusion that humans are male-dominant by nature (Lee, 1974). This strict comparison undermines the human social capacity for gender equity. Instead, building a three-way comparison of humans, chimpanzees, and bonobos might help us build a more accurate and representative human origin story based in shared power among males and females (Lee, 1974; de Waal, 2006).

Certainly, sustaining egalitarian romantic partnerships is pivotal to securing gender equity. The extent of paternal care varies across human cultures (Fernandez-Duque, Vallengia, & Mendoza, 2009). Nevertheless, to foster equality in the household, Western feminists have sought to redefine fathering that embodies the nurturing capacity of males (Silverstein, 1996). Egalitarian, socially monogamous gibbons and siamangs (Hylobatidae) show that females have considerable amounts of choice in who they mate with by displaying frequent events of extra-pair copulations (EPC: Kenyon et al., 2011; Lappan, 2007; Leighton, 2008; Palombit, 1994a; Palombit, 1994b; Reichard, 1995; Reichard, 2005; Reichard, 2009; Savini, Boesch, & Reichard, 2009). Despite their significant rates of EPC, female gibbons spend most of their time with their nuclear family unit (Liebal, Pika, & Tomasello, 2004). While equality is essential in sexual

relationships, it is also vital in relationships outside of a romantic partnership. In other words, gender equality must be established in not only women's personal lives but also broader political and social communities.

In Western patriarchal society, women have not yet gained social equality (Eagly & Carli, 2007). Bonobo's female-dominant social system suggest that female power reduces inequality. Rather than compete with one another for resources, female bonobos promote fairness by establishing friendly relationships with every individual in their group (Stevens et al. 2007; Ryu, Hill, & Furuichi, 2015; de Waal, 1995). Increased rates of sociosexual behavior, female coalitionary support, and affiliative intersexual relationships in matriarchal bonobos should encourage humans to consider an imperative transformation toward female dominance.

First, bonobos use sociosexual behavior to stimulate affiliative bonds (Furuichi, 1989; Idani, 1991; Moscovice et al., 2017, 2019; Ryu, Hill, & Furuichi, 2015; Tokuyama & Furuichi, 2016; Wrangham & Peterson, 1996). Sociosexual behavior is a common characteristic of haplorrhine primates (Sandel & Reddy, 2021), which includes great apes, monkeys, and tarsiers. Bonobos same-sex and intersexual sexual interactions reduce tension within their group (Furuichi, 1989; Idani, 1991; Moscovice et al., 2017, 2019; Ryu, Hill, & Furuichi, 2015; Stevens et al., 2006; Tokuyama & Furuichi, 2016; Wrangham & Peterson, 1996). While sex is the foundation for reproduction, sociosexual behavior transcends this narrow lens of heterosexuality to reduce tension, nurture social bonds, and promote pleasure (Ryu, Hill, & Furuichi, 2015; Sandel & Reddy, 2021; Small, 1992).

Second, maintaining strong affiliative relationships with unrelated females, strengthened by same-sex sexual interactions, is crucial to promoting cooperation and reducing male aggression (Moscovice et al., 2017, 2019; Ryu, Hill, & Furuichi, 2015). In the male-philopatric

community, all female bonobos are unrelated immigrants (Tokuyama, Sakamaki, & Furuichi, 2019). Yet, unrelated female coalitions are central to bonobo social organization (Parish, 1996; Tokuyama & Furuichi, 2016; Surbeck et al., 2017; Moscovice et al., 2017, 2019; Yasuo, 2020). Females leave their natal territory at sexual maturity and rely on affiliative bonds with unrelated females to be accepted in the coalition (Furuichi, 1989; Idani, 1991; Ryu, Hill, & Furuichi, 2015). Females nurture relationships based on experience and trust rather than competition (Wrangham & Peterson, 1996). Strengthened by same-sex sexual behavior (Moscovice et al., 2019; Ryu, Hill, & Furuichi, 2015), females rely on each other to avert male aggression (Wilson et al., 2014; Wrangham & Peterson, 1996) and subsequently promote peace.

Furthermore, in modern humans, affiliative interactions among unrelated females have also proved important to survival under patriarchy (Reynolds, 2021). Under patrilocal residence, whereby a female leaves her family to reside with the male partner's family, females form affiliative and cooperative bonds with unrelated females (Reynolds, 2021). They use reciprocal altruism to rely on each other for aid, information, and support (Reynolds, 2021). These female affiliative bonds might be disguised as a tactic to reduce intrasexual competition, but nonetheless, these female friendships are important for women to feel safe and advocated for in a foreign community (Reynolds, 2021). It is these female coalitions, or friendships, in both humans and bonobos, that allow females to defend themselves against overt male-dominance.

Third, significant intersexual affiliative bonds, among both related and unrelated individuals, are of equal importance to the central female coalitions (Stevens et al., 2006; Surbeck et al., 2019). Unlike chimpanzees who rarely form intersexual affiliative relationships outside the contexts of mating (Goodall, 1986; Gomes & Boesch, 2009; Matsumoto-Oda, 2002; Takahata, 1990), bonobo mothers encourage their sons to befriend unrelated females (Hohmann

et al., 1999). Females remain safe because of stable peaceful relationships between males and females. Bonobos demonstrate that affiliative bonds formed between males and females naturally encourages peaceful cooperation.

Bonobos are an example of where female-dominance selects for equitable relationships. Female bonobos cooperate to subvert male power and ensure that females have fair access to food resources. These female friendships in turn encourage males to befriend females. Even though female-dominance implies inequality, female power optimizes each sexes' reproductive success by promoting female's access to resources and male's access to females. Essentially, female bonobos foster equity.

Given that patriarchy is embedded into Western society, there must be a radical cultural shift that prioritizes women's claim to power. An egalitarian system, similar to that of the gibbons and siamangs, is unable to provide a model for gender equity because it is limited to a single social relationship (Liebal, Pika, & Tomasello, 2004). In contrast, humans form numerous social, romantic, and sexual relationships (Aureli et al., 2008). Therefore, gender equity is critical in *all* relationships. And while some might claim that the West has already reached an equal state between the sexes (Launius & Hassel, 2018), feminists' persistent activism indicates that gender equity has not been reached. The continuous pursuit toward gender equity is crucial to establish a just system for women and men.

Comparing species-specific social organizations among our closest living relatives, like the male-dominant chimpanzee, the female-dominant bonobo, and the egalitarian gibbon and siamang gives Westerners the opportunity to reorganize into an equitable society. Studying nonhuman animals, as opposed to human egalitarian and matrilineal societies, offers objectivity devoid of cultural constructs around gender. If we study social systems vastly different from our

own, we gain insight into how we might be able to solve the dilemma of gender inequity. The human androcentric narrative must end. By looking to the female-dominant bonobo, Western women can smash the patriarchy and protect every woman and man's right to a fair and just future.

CHAPTER VI: Women in primatology

"Primatology is politics by other means, and women's place is in the jungle, arguing the nature of beginnings and endings" (Haraway, 1984, p. 490).

Understanding the interactions between biological sex and socially constructed gender roles are central to reconstructing an equitable society. While "sex" refers to the different biological and physiological traits between males and females, "gender" refers to the socially constructed characteristics assigned to males and females (Deaux, 1985). Because of socially constructed gender schemas, women are obligated to navigate pervasive gender stereotypes in Western society. However, at least within scientific research disciplines, by and large, women have been more able than men to distinguish biological meanings from social meanings (Keller, 2000). The misogynistic norms in male-dominated fields restrict what women are allowed to achieve. Thus, women understand that society's expectations of their gender, rather than their sex, regulates their actions.

Because perceptions of gender depend largely on one's culture, not all women, and certainly not all men, are situated in their gender in the same way. Despite significant reform towards gender equity in the West, women have been routinely excluded from positions of power (Eagly & Carli, 2007). Yet, I hope that pattern is now changing and find some evidence for this in the United States electing its first woman Vice President, Kamala Harris, in 2020. Moreover, other non-Western communities, like matrilineal societies in south-central Africa, expect women to participate in politics and be active decision-makers in their communities (Robinson & Gottlieb, 2021). On the other hand, Western women must advocate for their own equal access to power among political, economic, and social institutions. Therefore, women

scientists, who face gendered structural barriers, are situated differently in the practice of science in general (Keller, 2000).

Primatology, for example, is a female-dominated, international scientific discipline. Primatology, a branch of modern biology and anthropology, highlights the roles of each sex in primate societies (Haraway, 1984). Prominent women scientists, such as Jane Goodall who studies chimpanzees, Dian Fossey who studied mountain gorillas, and Biruté Galdikas who studies Bornean orangutans, pioneered primatology. Previously, primatological research, led by men, focused on the role of males in primate societies. To represent primate societies more accurately, women primatologists shifted their focus on female primates. Moreover, primatology grew considerably around the same time as the “second wave” feminist movement (Haraway, 1984). While women primatologists sought to reconstruct the category of female, away from being based solely on maternal behavior, feminists sought to reconstruct the category of woman (Haraway, 1984). As the field expanded, other women primatologists, notably Dr. Sarah Blaffer Hrdy, intersected their sociobiologist and feminist identities to pave an inclusive and supportive path for other women to follow (Haraway, 1984).

Women primatologists’ narrative of female power in nonhuman primate societies influences the politics of gender in human societies (Haraway, 1984). Primatology has thus become a part of political discourse in the West, where “sex and gender structure knowledge” (Haraway, 1984, p. 492). Objectivity is no longer condemned in the domain of scientific investigation. Women and queer scientists today utilize their implicit bias to explore avenues of research that have been neglected, not because they were negligible, but because of the structural inequities within academia. Simply, “a broader range of people study a broader range of questions” (Rosenthal & Ryan, 2022, p. 1), thus leading to greater cumulative knowledge.

Women and men are challenged to walk a fine line of implicit bias that facilitates rather than hinders scientific discovery. Primatology, a female-dominated scientific discipline, models that implicit bias catechizes women's marginalization in modern society, to provoke a more equitable future for all people (Haraway, 1984). Ultimately, when women lead, diverse and representative equitable futures emerge.

Conclusion

“Politics only exists where there is more than one voice, more than one reality” (Haraway, 1984, p. 492).

Western patriarchal society exposes women to incessant gender inequality (Lorber, 2001). In the West, women experience greater economic, political, educational, and health-related disparities compared to men (Chant, 2006; Hausmann, 2009). For much of modern human history, under a false narrative, men thought that women were intellectually inferior (Darwin, 1871). Cultural misogyny, rather than biological theory, supported this false claim. For example, women in hunter-gatherer societies have always held powerful and influential economic roles (Hrdy, 1997; Lee, 1974).

Today, though Western women can hold political and economic leadership positions, the paths to secure these positions are increasingly onerous (Eagly & Carli, 2007). To ultimately secure gender equity, Western society must prioritize women’s power. Money and education influence an individual’s decision to participate in economic and political spheres (Verba & Nie, 1987). Therefore, when women have access to these resources, they are more likely engage in political and economic activities (Robinson & Gottlieb, 2021). While equality offers individuals the *same* opportunities, it often falls short in delivering truly equal outcomes because of historic and systemic male privileges conserved by patriarchy. Equity, on the other hand, ensures that *fair* opportunities effect equal outcomes to rectify systemic injustices (Cook & Hegtvedt, 1983).

Sociobiologists look to our closest living relatives to understand and explain human sociality. Humans, a species of great ape (Hominidae), are most closely related to chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*: Kovalaskas, Rilling, & Lindo, 2021). Despite patriarchal chimpanzees revealing much about the evolution of human aggressive behavior

(Wrangham, 1999), matriarchal bonobos display that female power leads to peace (Wilson et al., 2014).

Female-dominant bonobos (Parish, 1996; Parish & de Waal, 2000; Surbeck & Hohmann, 2013; Surbeck et al., 2019; Tokuyama & Furuichi, 2016) gain coalitionary support from unrelated females (Moscovice et al., 2017; Tokuyama & Furuichi, 2016). Unrelated females use same-sex sociosexual behavior to facilitate their formation into cooperate coalitions and avert male aggression (Furuichi, 1989; Idani, 1991; Moscovice et al., 2017, 2019; Ryu, Hill, & Furuichi, 2015; Tokuyama & Furuichi, 2016; Wrangham & Peterson, 1996). Because female coalitions wield so much power, to have greater access to mates, it pays off for young males to befriend older, unrelated females (Furuichi, 1997; Hohmann et al., 1999; Stevens et al., 2006). Affiliative bonds among females and between sexes are principal in reducing group tensions.

By contrast, social monogamy – as observed in gibbons (genera *Hylobates*, *Hoolock*, and *Nomascus*) and siamangs (genus *Symphalangus*) – is associated with egalitarianism (Emlen & Oring, 1977; Fuentes, 1998; Kleiman, 1977). While male gibbons and siamangs aid in parental care (Emlen & Oring, 1977; Fernandez-Duque, Valeggia, & Mendoza, 2009; Lappan, 2008; Rafacz, Margulis, & Santymire, 2012), females ultimately have considerable choice in *who* they mate with. Though they are socially monogamous, gibbons and siamangs are sexually promiscuous with significant rates of cheating, or extra-pair copulation (Kenyon et al., 2011; Lappan, 2007; Leighton, 2008; Palombit, 1994a; Palombit, 1994b; Reichard, 1995; Reichard, 2005; Reichard, 2009; Savini, Boesch, & Reichard, 2009). Despite their significant rates of cheating, gibbons and siamangs mostly affiliative with their nuclear family unit (Liebal, Pika, & Tomasello, 2004). Humans, on the other hand, rely on affiliative relationships both within and outside of their sexual partnerships (Amarasinghe & Amarasinghe, 2011; Lappan, 2007).

Egalitarianism persists insofar as the pair only affiliates with one another. Thus, gibbon and siamang's social system models equality for human sexual relationships but is insufficient in the fight for gender equity.

While bonobos are primarily female-dominant (Parish, 1996; Parish & de Waal, 2000; Surbeck & Hohmann, 2013; Surbeck et al., 2019; Tokuyama & Furuichi, 2016), females foster equity in their communities. With frequent rates of same-sex sociosexual behavior and high affinities for sharing among females (Furuichi, 1989; Idani, 1991; Moscovice et al., 2017, 2019; Ryu, Hill, & Furuichi, 2015; de Waal, 1995), female coalitions select for kinder males (Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016). With an equitable distribution of power among females and between mothers and sons (Surbeck, Mundry, & Hohmann, 2011), power in bonobo society is effectively shared among sexes. But, within female coalitions, females form a network of support and security and rely on shared power to maintain female dominance (Parish & de Waal, 2000; Vervafcke, de Vries, & van Elsacker, 2000b).

Primatology, a women-dominated scientific discipline, fosters equity with leading women researchers. Women primatologists, with the power to ask their own questions, highlight the critical role that females play in shaping primate social systems (Haraway, 1984). Thus, primatology bridges the gender gap within science and grants more power to women leaders. Primatology is an equitable field that uplifts diverse perspectives and allocates power to women, like relational feminism. Relational feminism, marked by general equality and greater female power that is neither male-centered nor female-centered, relieves male-dominated societies of gender inequity (Becker, 1999). Rather than conserve systems that continues to oppress women, racial and ethnic minorities, queers, and working- and lower- class people (Becker, 1999),

Western societies must reconstruct political and social systems that uphold women's equal right to power.

Women need power to advocate for their own needs. Women's power is pivotal in accumulating new knowledge and new definitions of equity. Without women primatologists and their biases, we would likely know very little about female-dominance in bonobos. With female support and male-female friendships, bonobos promote peace in an affiliative community. Bonobos extend a unique and compelling perspective on our human social capacity to establish an equitable society – one that eradicates the singular male voice and grants power to women.

LITERATURE CITED

- Achenbach, G. G., & Snowdon, C. T. (2002). Costs of caregiving: weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. *International Journal of Primatology*, 23(1), 179-189.
- Amarasinghe, N., & Amarasinghe, A. A. (2011). Social behaviours of captive *Hylobates moloch* (Primates: Hylobatidae) in the Javan gibbon rescue and rehabilitation center, Gedeh-Pangrango national park, Indonesia. *Taprobanica: The Journal of Asian Biodiversity*, 2(2).
- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., ... & Schaik, C. P. V. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology*, 49(4), 627-654.
- Bailey, N. W., & Zuk, M. (2009). Same-sex sexual behavior and evolution. *Trends in Ecology & Evolution*, 24(8), 439-446. doi:
- Barelli C, Heistermann M, Boesch C, Reichard U.H (2008). Mating patterns and sexual swellings in pair-living and multimale groups of wild white-handed gibbons *Hylobates lar*. *Animal Behavior*, 75:991–1001.
- Bearzi, M., & Stanford, C. (2010). A Bigger, Better Brain: Observations of chimpanzees and dolphins strengthen the notion that humanlike intelligence may not be uniquely human. *American Scientist*, 98(5), 402-409.
- Becker, M. (1999). Patriarchy and inequality: Towards a substantive feminism. *U. Chi. Legal F.*, 21.
- Blackwell, A. L. B. (1875). *The sexes throughout nature*. GP Putnam.
- Bleisch W.V., & Chen N (1991). Ecology and behavior of wild blackcrested gibbons (*Hylobates*

- concolor*) in China with a reconsideration of evidence for polygyny. *Primates*, 32:539–548.
- Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup conflicts among chimpanzees in Tai National Park: lethal violence and the female perspective. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, 70(6), 519-532.
- Bray, J., Pusey, A. E., & Gilby, I. C. (2016). Incomplete control and concessions explain mating skew in male chimpanzees. *Proceedings Biological Sciences*, 283(1842) doi:
- Brockelman, W. Y., Reichard, U., Treesucon, U., & Raemaekers, J. J. (1998). Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology*, 42(5), 329-339.
- Chant, S. (2006). *Re-visiting the "feminisation of Poverty" and the UNDP Gender Indices: What Case for a Gendered Poverty Index?*. Gender Institute.
- Chapman, S. N., Pettay, J. E., Lummaa, V., & Lahdenperä, M. (2019). Limits to fitness benefits of prolonged post-reproductive lifespan in women. *Current Biology*: 29(4), 645-650.e3.
- Connell, R., & Messerschmidt, J.W. (2005). Hegemonic masculinity: Rethinking the concept. *Gender & Society*, 19 (6), 829-859.
- Cook, K. S., & Hegtvedt, K. A. (1983). Distributive justice, equity, and equality. *Annual review of sociology*, 9(1), 217-241.
- Cunningham, C., & Mootnick, A. (2009). Gibbons. *Current Biology*, 19(14), R543-R544.
- Curie, M. (n.d.). *Quotable Quote*. Goodreads.
- <https://www.goodreads.com/quotes/16738-nothing-in-life-is-to-be-feared-it-is-only>.
- Darwin, C. (1859). *The origin of species*. P.F. Collier & Son.

- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. United Kingdom: D. Appleton.
- Deaux, K. (1985). Sex and gender. *Annual review of psychology*, 36(1), 49-81.
- Eagly, A. H. & Carli, L. L. (2007). *Through the labyrinth: The truth about how women become leaders*. Harvard Business Press.
- Eberhard, M. J. W. (1975). The evolution of social behavior by kin selection. *The Quarterly Review of Biology*, 50(1), 1-33.
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197(4300), 215-223.
- Emlen, S. T. (1995). An evolutionary theory of the family. *Proceedings of the National Academy of Sciences*, 92(18), 8092-8099.
- Feldblum, J. T., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Paiva, T., Cetinkaya-Rundel, M., ... & Gilby, I. C. (2014). Sexually coercive male chimpanzees sire more offspring. *Current Biology*, 24(23), 2855-2860.
- Fernandez-Duque, E., Vallengia, C. R., & Mendoza, S. P. (2009). The biology of paternal care in human and nonhuman primates. *Annual review of Anthropology*, 38, 115-130.
- Firman, R. C., Gasparini, C., Manier, M. K., & Pizzari, T. (2017). Postmating female control: 20 years of cryptic female choice. *Trends in Ecology & Evolution*, 32(5), 368-382.
- Fite, J. E., Patera, K. J., French, J. A., Rukstalis, M., Hopkins, E. C., & Ross, C. N. (2005). Opportunistic mothers: female marmosets (*Callithrix kuhlii*) reduce their investment in offspring when they have to, and when they can. *Journal of human evolution*, 49(1), 122-142.
- Foerster, S., Franz, M., Murray, C. M., Gilby, I. C., Feldblum, J. T., Walker, K. K., & Pusey, A.

- E. (2016). Chimpanzee females queue but males compete for social status. *Scientific Reports (Nature Publisher Group)*, 6, 35404. doi: 10.1038/srep35404.
- Furuichi, T. (1989). Social interactions and the life history of female *pan paniscus* in Wamba, Zaire. *International Journal of Primatology*, 10(3), 173-197.
- Furuichi, T. (1997). Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*, 18(6), 855-875.
- Gagneux, P., Gonder, M. K., Goldberg, T. L., & Morin, P. A. (2001). Gene flow in wild chimpanzee populations: what genetic data tell us about chimpanzee movement over space and time. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 356(1410), 889-897.
- Geissmann, T. (1991). Reassessment of age of sexual maturity in gibbons (*Hylobates* spp.). *American Journal of Primatology*, 23(1), 11-22.
- Geissmann, T., Rosenkranz-Weck, S., Van Der Loo, J., Orgeldinger, M., & Lameed, G. A. (2020). Taxon-Specific Pair Bonding in Gibbons (*Hylobatidae*).
- Gibbons, A. (1998). 'Monogamous' gibbons really swing. *Science*, 280(5364), 677.
- Gilby, I. C., Brent, L. J., 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.
- Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, 201, 1264-1266.
- Goodall, J. (1986). The chimpanzees of Gombe: Patterns of behavior. *Cambridge Mass.*
- Gomes, C. M., & Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-term basis. *PloS one*, 4(4), e5116.

- Graeber, D., & Wengrow, D. (2021). *The dawn of everything: A new history of humanity*. Farrar, Straus and Giroux.
- Haimoff, E.H., Yang XJ, He SJ, Chen N. (1986). Census and survey of wild black-crested gibbons (*Hylobates concolor concolor*) in Yunnan Province, People's Republic of China. *Folia Primatology*, 46:205–214.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of theoretical biology*, 7(1), 17-52.
- Haraway, D. J. (1984). Primatology is politics by other means. In *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* (Vol. 1984, No. 2, pp. 489-524). Philosophy of Science Association.
- Hausmann, R. (2009). "The global gender gap report 2009." World Economic Forum.
- He, J. (1999). A brief discussion on the essence and existing value of Mósuō culture. *Xue Shu Tan Suo* [in Chinese], 5(5), 60-62.
- He, Q., Wu, J., Ji, T., Tao, Y., & Mace, R. (2016). Not leaving home: Grandmothers and male dispersal in a duolocal human society. *Behavioral Ecology: Official Journal of the International Society for Behavioral Ecology*, 27(5), 1343-1352.
- Hohmann, G., Gerloff, U., Tautz, D., & Fruth, B. (1999). Social bonds and genetic ties: kinship association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour*, (9), 1219-1235.
- Hohmann, G., Mundry, R., & Deschner, T. (2009). The relationship between socio-sexual behavior and salivary cortisol in bonobos: tests of the tension regulation hypothesis. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, 71(3), 223-232.

- Holden, C. J., & Mace, R. (2003). Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1532), 2425-2433.
- hooks, b. (2000). *Feminist theory: From margin to center*. Pluto Press.
- Hrdy, S. B. (1997). Raising Darwin's consciousness: Female sexuality and the prehomimid origins of patriarchy. *Human Nature: An Interdisciplinary Biosocial Perspective*, 8(1), 1-49. doi: 10.1007/s12110-997-1003-9.
- Hrdy, S. B., & Judge, D. S. (1993). Darwin and the puzzle of primogeniture: an essay on biases in parental investment after death. *Human Nature*, 4, 1-1.
- Hutchins, E. (2008). The role of cultural practices in the emergence of modern human intelligence. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 363(1499), 2011-2019. doi: 10.1098/rstb.2008.0003.
- Hu, N., Guan, Z., Huang, B., Ning, W., He, K., Fan, P., & Jiang, X. (2018). Dispersal and female philopatry in a long-term, stable, polygynous gibbon population: Evidence from 16 years field observation and genetics. *American Journal of Primatology*, 80(9), N.PAG.
- Idani, G. (1991). Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatologica*, 57(2), 83-95.
- Ji, T., Wu, J. J., He, Q. Q., Xu, J. J., Mace, R., & Tao, Y. (2013). Reproductive competition between females in the matrilineal Mósuō of southwestern China. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1631), 20130081.
- Jiang, X., Wang, Y., Wang, Q. (1999). Coexistence of monogamy and polygyny in black-crested gibbon (*Hylobates concolor*). *Primates*, 40:607–611.
- Joseph, S. (1996). Patriarchy and development in the Arab world. *Gender & Development*, 4(2),

14-19.

- Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2008). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, 29(4), 931-947. doi: 10.1007/s10764-008-9276-3.
- Kanazawa, S., & Still, M. C. (1999). Why monogamy?. *Social forces*, 78(1), 25-50.
- Kano, T. (1996). Male rank order and copulation rate in a unit-group of bonobos at Wamba, Zaire. In W. C. McGrew, L. A. Marchant, & T. Nishida (Eds.), *Great ape societies*, (pp. 135–145). Cambridge, UK: Cambridge University Press.
- Keller, E. F. (2000). Women, gender, and science: Some parallels between primatology and developmental biology. In S. C. Strum & L. M. Fedigan (Ed.). *Primate encounters: Models of science, gender, and society* (pp. 382-397). University of Chicago Press.
- Kenyon, M., Roos, C., Binh, V. T., & Chivers, D. (2011). Extrapair paternity in golden-cheeked gibbons (*Nomascus gabriellae*) in the secondary lowland forest of Cat Tien National Park, Vietnam. *Folia Primatologica*, 82(3), 154-64. doi: 10.1159/000333143.
- Kleiman, D. G. (1977). Monogamy in mammals. *The Quarterly review of biology*, 52(1), 39-69.
- Klinkova, E., Hodges, J. K., Fuhrmann, K., Jong, T., & Heistermann, M. (2005). Male dominance rank, female mate choice and male mating and reproductive success in captive chimpanzees. *International Journal of Primatology*, 26(2), 357-484. doi: 10.1007/s10764-005-2929-6.
- Knauff, B. M., Abler, T. S., Betzig, L., Boehm, C., Dentan, R. K., Kiefer, T. M., ... & Rodseth, L. (1991). Violence and sociality in human evolution [and comments and replies]. *Current Anthropology*, 32(4), 391-428.
- Kovalaskas, S., Rilling, J. K., & Lindo, J. (2021). Comparative analyses of the Pan lineage reveal

- selection on gene pathways associated with diet and sociality in bonobos. *Genes, Brain and Behavior*, 20(3), e12715.
- Kuroda, S. (1980). Social behavior of the pygmy chimpanzees. *Primates*, 21(2), 181-197.
- Lappan S. (2005). Biparental care and male reproductive strategies in siamangs (*Symphalangus syndactylus*) in southern Sumatra [Ph.D. thesis]. *New York: Department of Anthropology, New York University; 2005.*
- Lappan, S. (2007). Social relationships among males in multimale siamang groups. *International Journal of Primatology*, 28:369–387.
- Lappan, S. (2008). Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. *Behavioral Ecology and Sociobiology*, 62(8), 1307-1317. doi: 10.1007/s00265-008-0559-7.
- Lancaster, J. B. (1968). On the Evolution of Tool-Using Behavior 1. *American Anthropologist*, 70(1), 56-66.
- 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.
- Lee, R. B. (1974). Male-female residence arrangements and political power in human hunter-gatherers. *Archives of Sexual Behavior*, 3(2), 167-173.
- Leighton, D. R. (2008). 12. Gibbons: Territoriality and Monogamy. *Primate societies* (pp. 135-145). University of Chicago Press.
- Lerner, G. (1986). The creation of patriarchy (Vol. 1). *Women and History*; V. 1.
- Lewis, H. M., Vinicius, L., Strods, J., Mace, R., & Migliano, A. B. (2014). High mobility

- explains demand sharing and enforced cooperation in egalitarian hunter-gatherers. *Nature Communications*, 5, 5789. doi: 10.1038/ncomms6789.
- Liebal, K., Pika, S., & Tomasello, M. (2004). Social communication in siamangs (*Symphalangus syndactylus*): use of gestures and facial expressions. *Primates*, 45(1), 41-57.
- Lorber, J. (2001). Gender inequality. Los Angeles, CA: Roxbury.
- Lorde, A. (2003). The master's tools will never dismantle the master's house. *Feminist postcolonial theory: A reader*, 25, 27.
- Lukas, D. & Huchard, E. (2014). The evolution of infanticide by males in mammalian societies. *Science*, 346(6211), 841-844.
- Macfarlane, G.F. & Vasey, P.L. (2016). Promiscuous primates engage in same-sex genital interactions. *Behavioral Processes*, 126, 21-26.
- Malenky, R. K. (1994). The significance of terrestrial herbaceous foods for bonobos, chimpanzees, and gorillas. *Chimpanzee cultures*, 59-75.
- Manson, J. H., Perry, S., & Parish, A. R. (1997). Nonconceptive sexual behavior in bonobos and capuchins. *International Journal of Primatology*, 18(5), 767-786.
- Matsumoto-Oda, A. K. I. K. O. (2002). Social relationships between cycling females and adult males in Mahale chimpanzees. *Behavioral diversity in chimpanzees and bonobos*, 168-180.
- Mattison, S. M. (2011). Evolutionary contributions to solving the "matrilineal puzzle". *Human Nature: An Interdisciplinary Biosocial Perspective*, 22(1-2), 64-88.
- Mattison, S., Moya, C., Reynolds, A., & Towner, M. C. (2018). Evolutionary demography of age

- at last birth: Integrating approaches from human behavioural ecology and cultural evolution. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 373(1743) doi: 2017.0060.
- McGrew, W. C. (1992). Chimpanzee material culture: implications for human evolution. *Cambridge University Press*.
- Miller, K. E., Bales, K. L., Ramos, J. H., & Dietz, J. M. (2006). Energy intake, energy expenditure, and reproductive costs of female wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology: Official Journal of the American Society of Primatologists*, 68(11), 1037-1053.
- Mitani, J. C. (1984). The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). *Behavioral Ecology and Sociobiology*, 15(3), 225-229.
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77(3), 633-640.
- Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal behaviour*, 59(4), 885-893.
- Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat?. *Animal Behaviour*, 61(5), 915-924.
- Mootnick, A. R., Baker, E., Nadler, R. D., & Merker, B. (2006). Hostile presenting in captive gibbons. *International Journal of Primatology*, 27(3), 809-825. doi: 10.1007/s10764-006-9040-5.
- 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 Lui Kotale, Salonga National Park, DRC. *American Journal of Physical Anthropology*, 163(1), 158-172.
- 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. doi: 10.1016/j.yhbeh.2019.104581.
- Murray, C. M., Wroblewski, E., & Pusey, A. E. (2007). New case of intragroup infanticide in the chimpanzees of Gombe National Park. *International Journal of Primatology*, 28(1), 23-37. doi: 10.1007/s10764-006-9111-7.
- Newton-Fisher, N. (2006). Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. *International Journal of Primatology*, 27(6), 1589-1599. doi: 10.1007/s10764-006-9087-3.
- Newton-Fisher, N. E., Thompson, M. E., Reynolds, V., Boesch, C., & Vigilant, L. (2010). Paternity and Social Rank in Wild Chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, 142(3), 417-428. doi:10.1002/ajpa.21241.
- Osvath, M., & Osvath, H. (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: Self-control and pre-experience in the face of future tool use. *Animal Cognition*, 11(4), 661-74. doi: 10.1007/s10071-008-0157-0.
- Page, A. E., Chaudhary, N., Viguiere, S., Dyble, M., Thompson, J., Smith, D., ... & Migliano, A. B. (2017). Hunter-gatherer social networks and reproductive success. *Scientific reports*, 7(1), 1-10.

- Palombit, R. A. (1992). Pair bonds and monogamy in wild siamang (*Hylobates syndactylus*) and white-handed gibbon (*Hylobates lar*) in northern Sumatra (Doctoral dissertation, University of California, Davis).
- Palombit, R.A. (1994a). Dynamic pair bonds in hylobatids: Implications regarding monogamous social systems. *Behaviour*. 1994;128:65-101. doi: 10.1163/156853994x00055.
- Palombit, R.A. (1994b). Extra-pair copulations in a monogamous ape. *Animal Behaviour*. 1994;47:721-723. doi: 10.1006/anbe.1994.1097.
- Palombit, R. A. (1995). Longitudinal patterns of reproduction in wild female siamang (*Hylobates syndactylus*) and white-handed gibbons (*Hylobates lar*). *International Journal of Primatology*, 16(5), 739-760.
- Palombit, R. A. (1997). Inter-and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*). *Folia Primatologica*, 68(6), 321-337.
- Palombit, R. A. (1999). Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 7(4), 117-129.
- Parish, A. R. (1996). Female relationships in bonobos (*pan paniscus*): Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Human Nature* (Hawthorne, N.Y.), 7(1), 61-96. doi: 10.1007/bf02733490.
- Parish, A. R., & de Waal, F. B. (2000). The other "closest living relative:" How bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and intersexual interactions, and hominid evolution. *Annals of the New York Academy of Sciences*, 907, 97-113.

- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological reviews*, 45(4), 525-567.
- Parker, S., & Parker, H. (1979). The myth of male superiority: Rise and demise. *American Anthropologist*, 81(2), 289-309.
- Pepper, J. W., Mitani, J. C., & Watts, D. P. (1999). General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, 20(5), 613-632.
- Phiri, K.M. (1983). Some changes in the matrilineal family system among the Chewa of Malawi. *Journal of African History*, 24 (2), 257–274.
- Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: suspiciously human?. *Trends in cognitive sciences*, 7(4), 157-160.
- Prum, R. O. (2017). *The evolution of beauty: How Darwin's forgotten theory of mate choice shapes the animal world-and us*. Anchor.
- Pusey, A., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, 277(5327), 828-831.
- Pusey, A., Murray, C., Wallauer, W., Wilson, M., Wroblewski, E., & Goodall, J. (2008). Severe aggression among female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania. *International Journal of Primatology*, 29(4), 949-973. doi: 10.1007/s10764-008-9281-6.
- Pusey, A. E., & Schroepfer-Walker, K. (2013). Female competition in chimpanzees. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 368(1631), 20130077. doi: 10.1098/rstb.2013.0077.
- Queller, D. C. (1992). A general model for kin selection. *Evolution*, 46(2), 376-380.

- Rafacz, M. L., Margulis, S. U. E., & Santymire, R. M. (2012). Hormonal Correlates of Paternal Care Differences in the Hylobatidae. *American Journal of Primatology*, 74(3), 247-260.
- Reichard, U. (1995). Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology*, 100(2), 99-112.
- Reichard, U. H. (2003). Social monogamy in gibbons: the male perspective. *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press, Cambridge, 190-213.
- Reichard, U.H. (2009). The social organization and mating system of Khao Yai white-handed gibbons: 1992-2006. In: Lappan S, Whittacker DJ, editors. *The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology*, New York: Springer; 2009. p. 347-384.
- Reichard, U. H., Ganpanakngan, M., & Barelli, C. (2012). White-handed gibbons of Khao Yai: social flexibility, complex reproductive strategies, and a slow life history. In *Long-term field studies of primates* (pp. 237-258). Springer, Berlin, Heidelberg.
- Reichert, K. E., Heistermann, M., Hodges, J. K., 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. doi: 10.1046/j.1439-0310.2002.00798.x.
- Richardson, D. (1993). Sexuality and male dominance. *Introducing Women's Studies* (pp. 74-98). Palgrave Macmillan, London.
- Riedel, J., Franz, M., & Boesch, C. (2011). How feeding competition determines female chimpanzee gregariousness and ranging in the Tai National Park, Côte d'Ivoire. *American Journal of Primatology*, 73(4), 305-313.

- Roberts, A. I., & Bradley Roberts, S. G. (2015). Gestural communication and mating tactics in wild chimpanzees. *PLoS One*, 10(11) doi: 10.1371/journal.pone.0139683.
- Robinson, A. L., & Gottlieb, J. (2021). How to close the gender gap in political participation: Lessons from matrilineal societies in Africa. *British Journal of Political Science*, 51(1), 68–92.
- Rosenthal, G. G., & Ryan, M. J. (2022). Sexual selection and the ascent of women: Mate choice research since Darwin. *Science*, 375(6578), eabi6308.
- Ryu, H., Hill, D. A., & Furuichi, T. (2015). Prolonged maximal sexual swelling in wild bonobos facilitates affiliative interactions between females. *Behaviour*, 152(3/4), 285–311.
- Schatz, E (2002). Numbers and narratives: Making sense of gender and context in rural Malawi. PhD Dissertation. Philadelphia: University of Pennsylvania.
- Shepherd, W. T. (1915). Some observations on the intelligence of the chimpanzee. *Journal of Animal Behavior*, 5(5), 391.
- Silverstein, L. B. (1996). Fathering is a feminist issue. *Psychology of Women Quarterly*, 20(1), 3-37.
- Small, M. F. (1992). The evolution of female sexuality and mate selection in humans. *Human Nature*, 3(2), 133-156.
- Smucny, D. A., Abbott, D. H., Mansfield, K. G., Schultz-Darken, N. J., Yamamoto, M. E., Alencar, A. I., & Tardif, S. D. (2004). Reproductive output, maternal age, and survivorship in captive common marmoset females (*Callithrix jacchus*). *American Journal of Primatology: Official Journal of the American Society of Primatologists*, 64(1), 107-121.
- Stevens, J. M. G., Vervaecke, H., Vries, H. D., & Linda, V. E. (2006). Social structures in *Pan*

- paniscus*: Testing the female bonding hypothesis. *Primates*, 47(3), 210-7. doi: 10.1007/s10329-005-0177-1.
- Stevens, J. M., Vervaecke, H., De Vries, H., & van Elsacker, L. (2007). Sex differences in the steepness of dominance hierarchies in captive bonobo groups. *International Journal of Primatology*, 28(6), 1417-1430.
- Strum, S. C., & Fedigan, L. M. (Eds.). (2000). *Primate encounters: models of science, gender, and society*. University of Chicago Press.
- Surbeck, M., Boesch, C., Girard-Buttoz, C., Crockford, C., Hohmann, G., & Wittig, R. M. (2017). Comparison of male conflict behavior in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), with specific regard to coalition and post-conflict behavior. *American Journal of Primatology*, 79(6), e22641.
- Surbeck, M., Boesch, C., Crockford, C., Thompson, M. E., Furuichi, T., Fruth, B., ... & Langergraber, K. (2019). Males with a mother living in their group have higher paternity success in bonobos but not chimpanzees. *Current Biology*, 29(10), R354-R355.
- 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.
- 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.
- Takahata, Y. (1990). Adult males' social relations with adult females. *The chimpanzees of the Mahale Mountains: sexual and life history strategies*. University of Tokyo Press, Tokyo, 133-148.

- Tardif, S. D., Ziegler, T. E., Power, M., & Layne, D. G. (2005). Endocrine changes in full-term pregnancies and pregnancy loss due to energy restriction in the common marmoset (*Callithrix jacchus*). *The Journal of Clinical Endocrinology & Metabolism*, 90(1), 335-339.
- Tocheri, M. W., Orr, C. M., Jacofsky, M. C., & Marzke, M. W. (2008). The evolutionary history of the hominin hand since the last common ancestor of *Pan* and *Homo*. *Journal of Anatomy*, 212(4), 544-562.
- 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. doi: 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. doi: 10.1002/ajpa.23929.
- Trivers, R. L. (1972). *Parental investment and sexual selection* (pp. 136-179). Routledge.
- Turner, E. R. (1913). The Women's Suffrage Movement in England. *American Political Science Review*, 7(4), 588-609.
- van Schaik, C. P., & Kappeler, P. M. (1997). Infanticide risk and the evolution of male-female association in primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264(1388), 1687-1694.
- van Schaik, C. P. (2000). Infanticide by male primates: The sexual selection hypothesis revisited. *Infanticide by Males and Its Implications*, Cambridge University Press, Cambridge, pp. 27-60.

- Vasey, P. L. (1995). Homosexual behavior in primates: A review of evidence and theory. *International Journal of Primatology*, 16(2), 173-204.
- Verba, S., & Nie, N. H. (1987). Participation in America: Political democracy and social equality. *University of Chicago Press*.
- Vervaecke, H., De Vries, H. A. N., & Van Elsacker, L. (2000a). Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus*). *International Journal of Primatology*, 21(1), 47-68.
- Vervaecke, H., De Vries, H., & van Elsacker, L. (2000b). Function and distribution of coalitions in captive bonobos (*Pan paniscus*). *Primates*, 41(3), 249-265.
- de Waal, F. B. M. (1987). Tension regulation and nonreproductive functions of sex in captive bonobos (*Pan paniscus*). *Nat Geogr Res*, 3(3), 318-335.
- de Waal, F. B. (1995). Bonobo sex and society. *Scientific American*, 272(3), 82-88.
- de Waal, F. B. (2005). A century of getting to know the chimpanzee. *Nature*, 437(7055), 56-59.
- de Waal, F. B. (2007). *Chimpanzee politics: Power and sex among apes*. JHU Press.
- Wallis, J. (1992). Chimpanzee genital swelling and its role in the pattern of sociosexual behavior. *American Journal of Primatology*, 28(2), 101-113.
- Watts, D. P. (2007). Effects of male group size, parity, and cycle stage on female chimpanzee copulation rates at Ngogo, Kibale National Park, Uganda. *Primates*, 48(3), 222-31. doi:
- Wen, B., Shi, H., Ren, L., Xi, H., Li, K., Zhang, W., ... & Xiao, C. (2004). The origin of Mosuo people as revealed by mtDNA and Y chromosome variation. *Science in China Series C: Life Sciences*, 47(1), 1-10.
- 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. doi:

- Wilson, E. O. (2000). *Sociobiology: The new synthesis*. Harvard University Press.
- Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., . . . Wrangham, R. W. (2014). Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*, 513(7518), 414-7. doi: 10.1038/nature13727.
- Wittenberger, J. F., & Tilson, R. L. (1980). The evolution of monogamy: hypotheses and evidence. *Annual review of ecology and systematics*, 11(1), 197-232.
- Wittiger, L., & Boesch, C. (2013). Female gregariousness in western chimpanzees (*Pan troglodytes verus*) is influenced by resource aggregation and the number of females in estrus. *Behavioral Ecology and Sociobiology*, 67(7), 1097-1111. doi: 10.1007/s00265-013-1534-5.
- Woodburn, J. (1982). Egalitarian societies. *Man*, 431-451.
- Wrangham, R. W. (1987). The significance of African apes for reconstructing human social evolution. *The evolution of human behavior: Primate models*, 51-71.
- Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology*, 110(S29), 1-30.
- Wrangham, R. W., & Peterson, D. (1996). *Demonic males: Apes and the origins of human violence*. Mariner Books.
- Wrangham, R. W., & Glowacki, L. (2012). Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers. *Human Nature: An Interdisciplinary Biosocial Perspective*, 23(1), 5-29. doi: 10.1007/s12110-012-9132-1.
- Wrangham, R. W. (2018). Two types of aggression in human evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 115(2), 245.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., &

- Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal behaviour*, 77(4), 873-885.
- You, Z. (1997). The History of Nationalities in Yunnan (in Chinese). *Kunming: Yunnan University Press*, 19-29.