

**The Social and Reproductive Behavior of Male Chimpanzees
in Gombe National Park, Tanzania**

by

Joseph Taliaferro Feldblum

Department of Evolutionary Anthropology
Duke University

Date _____

Approved:

Anne E. Pusey, Ph.D., Supervisor

Susan Alberts, Ph.D.

Steven Churchill, Ph.D.

Ian C. Gilby, Ph.D.

Brian Hare, Ph.D.

James W. Moody, Ph.D.

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Evolutionary Anthropology in the Graduate School
of Duke University

2017

ABSTRACT

The Social and Reproductive Behavior of Male Chimpanzees

in Gombe National Park, Tanzania

by

Joseph Taliaferro Feldblum

Department of Evolutionary Anthropology
Duke University

Date _____

Approved:

Anne E. Pusey, Ph.D., Supervisor

Susan Alberts, Ph.D.

Steven Churchill, Ph.D.

Ian C. Gilby, Ph.D.

Brian Hare, Ph.D.

James W. Moody, Ph.D.

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Evolutionary Anthropology in the Graduate School
of Duke University

2017

Copyright by
Joseph Taliaferro Feldblum
2017

Abstract

This dissertation presents three studies of the social and reproductive behavior and social structure of male chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania.

I. In many species of non-human primates, males cooperate and form friendly social bonds while simultaneously competing with each other for dominance rank and mating opportunities. While several studies reveal clear links between female bonds and correlates of fitness in female philopatric primate species, few have investigated whether bonds among males have measurable fitness benefits. Further, no studies in chimpanzees have investigated the fitness effects of cooperative exchange, or contrasted the fitness effects of bond formation and cooperative exchange. Here, I investigate whether 1) male social bonds, 2) position in affiliative and coalition networks, or 3) strategic exchange with other individuals of grooming for support or tolerance facilitate fitness benefits in one population of wild, free-ranging chimpanzees. I generated measures of social connectedness, coalition formation, and grooming effort for each male in two-year periods from 1990 to 2011, and employed mixed models to determine whether, controlling for current rank and age, these measures predicted 1) rank change (a correlate of future reproductive output) and 2) reproductive success within each period. I found that rank change was associated with betweenness in the network of coalition formation, but only weakly with social bonds and not at all with position in the network of social relationships. I further found that rank change was predicted by grooming

effort, although this relationship depended on male dominance rank. Surprisingly, reproductive success was not associated with social connectedness or with betweenness in coalitionary or social relationship networks. Instead, grooming effort strongly predicted reproductive success. Thus it appears that males that occupy central positions in the coalition network, and those that groom others at a high rate, are more likely to rise in rank (if they are low-ranking to begin with). However, males that successfully sire offspring groom others at a high rate. These results suggest that, unlike in cercopithecine primates, social bonds do not enhance fitness in male chimpanzees, and instead males rely on grooming and coalition formation to improve their rank and reproductive success.

II. Animals face both costs and benefits associated with living in groups. When the costs of membership exceed the benefits, group fissions can occur. Fissions are documented in a number of animal species, but are comparatively rare in male philopatric primates. One of the few likely cases occurred in chimpanzees in 1973 in Gombe National Park, Tanzania, when the main study community split into two separate communities, Kasekela and Kahama. Over the next four years, the Kasekela community killed the adult males and one female of the Kahama community. Here we use social network analysis to explore the process of community fission in chimpanzees by examining association, grooming, and ranging patterns. We found that the two communities split from one original cohesive community, although one with incipient subgrouping patterns. Subgrouping patterns in the grooming and association networks began to increase sharply beginning in 1971, and this period closely coincided with a

dominance struggle between three high-ranking males and with a peak in operational sex ratio. Finally, we found a relationship between post-split community membership and previous association, grooming and ranging patterns in most periods of analysis, a tendency that became more pronounced as the fission approached. Thus, analysis suggests that the community began to split during a time of unusual sex ratio and a protracted dominance struggle, and that individuals remained with others with whom they preferentially associated in the previous years. These results are contrasted with group fissions in other taxa, and provide clues to the costs and benefits of group membership in chimpanzees.

III. In sexually reproducing animals, male and female reproductive strategies often conflict. In some species, males use aggression to overcome female choice, but debate persists over the extent to which this strategy is successful. Previous studies of male aggression toward females among wild chimpanzees have yielded contradictory results about the relationship between aggression and mating behavior. Critically, however, copulation frequency in primates is not always predictive of reproductive success. We analyzed a 17-year sample of behavioral and genetic data from the Kasekela chimpanzee community in Gombe National Park, Tanzania, to test the hypothesis that male aggression toward females increases male reproductive success. We examined the effect of male aggression toward females during ovarian cycling, including periods when the females were sexually receptive (swollen) and periods when they were not. We found that, after controlling for confounding factors, male aggression during a female's swollen

periods was positively correlated with copulation frequency. However, aggression toward swollen females was not predictive of paternity. Instead, aggression by high-ranking males toward females during their nonswollen periods was positively associated with likelihood of paternity. This indicates that long-term patterns of intimidation allow high-ranking males to increase their reproductive success, supporting the sexual coercion hypothesis. To our knowledge, this is the first study to present genetic evidence of sexual coercion as an adaptive strategy in a social mammal.

To my wonderful family, friends, and fiancée.

To Bill Boatwright, who combined brilliance, good cheer and terrible jokes into a single improbable avuncular package.

Table of Contents

Abstract.....	iv
Table of Contents.....	ix
List of Tables	xii
List of Figures.....	xiii
Acknowledgements.....	xiv
1. Introduction.....	1
1.1 Relationships between males: competition and cooperation.....	4
1.1.1 Competition between males	4
1.1.2 Cooperation and social bonds between males	7
1.1.3 Studies of male relationships in this dissertation	10
1.2 Male-female sexual conflict	11
1.2.1 Studies of sexual conflict in this dissertation	15
2. The adaptive value of male relationships in the chimpanzees of Gombe National Park, Tanzania.....	16
2.1 Introduction	16
2.2 Methods.....	20
2.2.1 Study site and data.....	20
2.2.2 Rank change analyses.....	28
2.2.3 Reproductive success analyses.....	29
2.3 Results	30
2.3.1 Rank Change analyses.....	30

2.3.2 Reproductive Success analyses	36
2.4 Discussion	41
3. Social network analysis reveals the timing and causes of a unique chimpanzee community fission: Gombe's Four Years' War	46
3.1 Introduction	46
3.2 Methods	52
3.2.1 Subgrouping analyses:.....	54
3.2.2 Ranging data:.....	55
3.2.3 Modelling community co-membership vs. association and grooming.....	56
3.2.4 Identification of potential catalysts	57
3.3 Results	59
3.3.1 Subgrouping Analyses.....	59
3.3.2 Ranging	63
3.3.3 Association patterns and group membership.....	64
3.3.4 Potential catalysts	65
3.4 Discussion	66
4. Sexually Coercive Male Chimpanzees Sire More Offspring.....	73
4.1 Summary	73
4.2 Results	74
4.2.1 Aggression and Paternity.....	74
4.2.2 Aggression and Copulation	78
4.2.3 Timing of Male-Female Aggression	80

4.2.4 Copulation and Paternity	80
4.3 Discussion	81
4.4 Experimental Procedures.....	85
4.4.1 Analyses	87
2.4.1.1 Paternity	89
2.4.1.2 Copulation Rate	89
2.4.1.3 Copulation Rate versus Likelihood of Paternity	89
5. Conclusions and future directions.....	91
5.1 Future work emerging from Chapter 2.....	91
5.2 Future work emerging from Chapter 3.....	95
5.3 Future work emerging from Chapter 4.....	96
5.4 Forward	98
Appendix A: Supplementary figures and tables	99
References.....	104
Biography.....	132

List of Tables

Table 1: The best “CSI-only” model for predicting rank change	31
Table 2: The best models predicting rank change.....	33
Table 3: Factors predicting reproductive success in “CSI-only” models.....	37
Table 4: The best models for predicting reproductive success	39
Table 5: Modularity Optimizing Algorithm results	60
Table 6: QAP results.....	63
Table 7: Models and effect sizes for averaged model and all models with $\Delta AICc \leq 2$	76
Table 8: Models and effect sizes for the average model and the best 10 models.	79
<u>Appendix A:</u>	
Table 9: Best models predicting rank change using frequency-based measures of grooming effort and CSI.	100
Table 10: Best models for predicting rank change using rate-based measures and including betweenness in the network of coalition formation	101
Table 11: Best models for predicting reproductive success, coalitions dataset	102
Table 12: Betweenness in the male affiliative networks	103

List of Figures

Figure 1: Age of male sires vs. male survival.....	26
Figure 2: Rank change vs. sociality	31
Figure 3: Predicted rank change over a two year period (with confidence regions) vs. rate of received grooming, for males of low, middle, and high rank. Points are partial residuals.	34
Figure 4: Predicted rank change over a two year period (with confidence regions) vs. rate of received grooming, for males of low, middle, and high rank. Points are partial residuals	35
Figure 5: Predicted rank change vs. betweenness in the network of coalition formation.....	36
Figure 6: Predicted likelihood of siring offspring vs. rate of grooming others at three levels of male rank.....	40
Figure 7: Predicted likelihood of siring offspring vs. rate of received grooming	41
Figure 8: Timelines of modularity, ranging patterns and potential catalysts during the study period.	61
Figure 9: Networks of joint arrivals among males in each 6-month window.....	62
Figure 10: Average male range position in Gombe National Park in the 6-month periods for which we have ranging data.....	64
Figure 11: Predicted likelihood of paternity based on covariates from the best model.	77
Figure 12: Paternity among highly-ranked males by non-swollen aggression rate	81

Acknowledgements

Data collection was supported primarily by the Jane Goodall Institute (JGI), with additional support from the National Science Foundation (NSF) (LTREB-1052693) and the National Institutes of Health (NIH) (R01 AI 058715). Digitization and analysis of behavioral and genetic data were supported by grants from the NSF (DBS-9021946, SBR-9319909, BCS-0452315, BCS-0648481, and LTREB-1052693), the NIH (R01 AI 058715), the University of Minnesota, the Harris Steel Group, the Windibrow Foundation, the Jane Goodall Institute, the Carnegie Corporation, and Duke University. I thank Jane Goodall for permission to work with the long-term data and Tanzania National Parks, Tanzania Wildlife Research Institute, and Tanzania Commission for Science and Technology for permission to work in Gombe National Park. All data collection was approved by these Tanzanian bodies and the Duke University Institutional Animal Care and Use Committee. I further thank Esther Collins for translation, and Joann Schumacher-Stankey and numerous indefatigable Duke undergraduate students for data extraction. The work presented here was generously supported by the NSF Graduate Research Fellowship Program (DGE-1106401), the L. S. B. Leakey Foundation, Conservation International, and Duke University.

I am very grateful to the wonderful Gombe Stream Research Center staff for their heroic data collection, warm companionship and good humor, and their saintly patience for an Mzungu Pori with subpar Swahili. I thank Kassim Sadick, Zozo, Hamimu, and Hashim Salala for being indispensable field assistants and friends in Gombe, for teaching

me to navigate the treacherous park terrain, and for helping me lose some of my fear of snakes. Finally, I thank Drs. Deus Mjungu and Anthony Collins for their critical support and companionship, for late-night Arsenal games, and discussion of the Grateful Dead in the most improbable of places.

For friendship and support in the field and back home, and invaluable intellectual partnership, I gratefully thank Kara Walker and Emily Boehm. I further thank my other field companions Jordan Miller, for her strict application of the rules; Kaitlin Wellens, with whom I share a bond etched in scar tissue on our respective backs forever; and Alejandra Pascual-Garrido, who helped me through my malaria scare.

I also thank colleagues at Duke and elsewhere for thoughtful comments and invaluable technical advice on the projects presented here, particularly Steffen Foerster, Mathias Franz, Amanda Lea, Charlie Nunn, Joan Silk, Martin Muller, Melissa Emery-Thompson, Richard Wrangham, Zarin Machanda, Elizabeth Lonsdorf, Catherine Markham, Carson Murray, Maggie Stanton, Peter Mucha, Aaron Sandel, Rachna Reddy, India Schneider-Crease, Jackson Spradley, and Randi Griffin.

I am grateful to my dissertation committee, Drs. Susan Alberts, Steve Churchill, Ian Gilby, Brian Hare, and Jim Moody, for their perspectives, advice, and criticism throughout my graduate career. I am especially grateful to Dr. Anne Pusey, my primary advisor, for her brilliant advice and her gentle but firm guidance.

This work would not be possible without the loving support of my parents, Tolly Boatwright and Paul Feldblum, and their dogged insistence that I learn to think and write

with clarity and care. The belief that one can produce original and worthwhile scholarship is hard to come by, and I'm lucky to have parents who helped foster that belief, both by pushing me and by modelling a full life of the mind. I am also grateful to my brother, Sammy Feldblum, a brilliant and curious scholar, engaging raconteur, and surprisingly good rapper, for intellectual support and being that dude.

For perspective and balance, I will be forever grateful to the students and teachers of Lee County High School in Marianna, Arkansas. No job will ever be as important or rewarding as my position teaching math to my group of brilliant, incorrigible, hilarious students. Nor will any position, academic or otherwise, ever feel difficult in comparison.

Amelia O'Rourke-Owens was a loving and infinitely patient partner throughout the writing of this dissertation, and progress would have ground to a halt without her saintly support down the stretch. In a strange way, that she would let me off the dishwashing and cooking hook to help me finish is perhaps the truest sign of love she has ever offered me.

Numerous colleagues have contributed in various ways to my research. I gratefully list them below, together with their specific contributions.

Chapter 2

Christopher Krupenye	Contributed to the creation of initial dataset of male sociality, contributed to study design, reviewed and edited the manuscript
----------------------	---

Ian C. Gilby Developed long-term Gombe database, contributed to study design, reviewed and edited the manuscript

Anne E. Pusey Created and developed long-term Gombe database, contributed to study design, reviewed and edited the manuscript

Chapter 3

Sofia Manfredi Extracted data from the long-term data and generated data sets

Ian C. Gilby Developed long-term Gombe database, contributed to study design, reviewed and edited the manuscript

Anne E. Pusey Created and developed long-term Gombe database, contributed to study design, reviewed and edited the manuscript

Chapter 4

Emily E. Wroblewski Assigned paternities and calculated relatedness values; contributed to, reviewed and edited the manuscript

Rebecca S. Rudicell Assigned paternities and calculated relatedness values

Beatrice H. Hahn Assigned paternities and calculated relatedness values

Thais Paiva Implemented regression analyses

Mine Cetinkaya-Rundel Implemented regression analyses

Anne E. Pusey

Created and developed long-term Gombe database,
contributed to study design, reviewed and edited the
manuscript

Ian C. Gilby

Developed long-term Gombe database, contributed to study
design, reviewed and edited the manuscript

Simia quam similis turpissima bestia nobis!

“The ape, vilest of beasts, how like to us!”

- Ennius, 2nd c. BCE

1. Introduction

Across the animal kingdom, living in groups is a widespread solution to the challenges of survival and reproduction. Group living is hypothesized to protect against predation and infanticide, facilitate territorial defense, aid in finding mates, and improve foraging and hunting efficiency (Alexander, 1974; Dunbar, 1988; Krause & Ruxton, 2002; Pitcher, Magurran, & Winfield, 1982; van Schaik & Kappeler, 1997). However, group living presents an additional set of challenges: members of groups must compete for access to food and mates, and are more likely to be exposed to socially-transmitted pathogens (Alexander, 1974; Altizer et al., 2003; Andersson, 1994; Dunbar, 1988; Krause & Ruxton, 2002; Møller, Dufva, & Allander, 1993). Thus to enjoy the benefits of group membership, social animals must maintain cohesion with group-mates despite competing with them for resources (Krause & Ruxton, 2002). These competing interests produce a complex combination of cooperation and competition within and between groups that interact to influence individual fitness and shape social structure.

In most species of social mammals, males disperse at sexual maturity (Greenwood, 1980; Pusey & Packer, 1987a), most probably to avoid the costs of inbreeding and competition with kin (Gandon, 1999; Perrin & Mazalov, 1999, 2000). This pattern of dispersal yields groups wherein females tend to be more closely related to each other, and consequently more social, than are males. Males, in turn, compete for access to females. This pattern is common among primates, particularly cercopithecines (e.g. ringtail lemurs, *Lemur catta*: Sussman, 1992; capuchin monkeys, *Cebus capucinas*: Jack & Fedigan, 2004; savannah baboons, *Papio cynocephalus*: Alberts, 1995; reviewed

in: Kapsalis, 2003). Chimpanzees, however, exhibit significantly different patterns of dispersal and sociality, and thus present an opportunity to test some of the underlying assumptions of hypotheses regarding sociality.

Unusually among primates and other mammals, chimpanzees display the pattern of male philopatry and female dispersal (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida & Kawanaka, 1972; Pusey, 1979). Researchers have suggested that in eastern chimpanzees (*Pan troglodytes schweinfurthii*), ecology and the exigencies of maternal care together increase the costs of grouping for females beyond those for males, which selects against female gregariousness (Wrangham, 2000). Females establish “core areas”, where they spend much of their time when alone and presumably have a foraging advantage (Miller et al., 2013; Pusey & Schroepfer-Walker, 2013; Williams, Pusey, Carlis, Farm, & Goodall, 2002; Wrangham & Smuts, 1980). Males in turn cooperate to defend a larger territory that includes the ranges of many females (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Goodall et al., 1979; Manson & Wrangham, 1991; Mitani, Watts, & Amstler, 2010; Pusey, 1979; Sugiyama, 2004; Wrangham, 1979).

Recent research suggests that territorial expansion is associated with increased food availability and reduced inter-birth intervals for females within the group (Williams, Oehlert, Carlis, & Pusey, 2004). Accordingly, territorial competition is intense. Competition between groups can impose heavy costs on individuals, including severe wounding and death (Manson & Wrangham, 1991; Wilson et al., 2014; Wrangham, 1999). Because of these costs, and the fact that group size is associated with success in territorial competition (Manson & Wrangham, 1991; Mjungu, Wilson, Foerster, & Pusey,

2015; Wrangham, 1999), chimpanzee territoriality likely selects for adaptations that allow individuals to live in large groups.

Indeed, among eastern chimpanzees, males are generally more gregarious than females, cooperate in a range of contexts, and form strong and enduring social bonds (Gilby & Wrangham, 2008; Goodall, 1986; Mitani, 2009; Muller & Mitani, 2005; Pepper, Mitani, & Watts, 1999; Wrangham & Smuts, 1980), although sex differences in gregariousness are less pronounced at some sites (Lehmann & Boesch, 2008; Sugiyama, 1988; Wakefield, 2008). Moreover, when the external pressure of between-group competition is relaxed due to community isolation, male tolerance and cooperation can be significantly reduced (Sugiyama, 1999, 2004). Nevertheless, there are likely additional benefits to male sociality; males cooperate strategically with select community members in order to compete for access to females within their social groups (Muller & Mitani, 2005).

Another adaptation that facilitates the formation of large groups is fission-fusion social organization, whereby chimpanzees form temporary and fluid subgroups, or “parties”, that vary in composition over the course of a day (Boesch & Boesch-Achermann, 2000; Chapman, Chapman, & Wrangham, 1995; Goodall, 1986). Because it means that every member of a community is rarely together at once, this social organization may allow chimpanzees to avoid some of the costs normally associated with large group size, such as increased feeding and mate competition. In the extreme, large group size may produce more long-term (though still incomplete) subgrouping, as seen in the “neighborhoods” in the unusually large Ngogo community in Kibale National Park,

Uganda (Mitani & Amstler, 2003).

Yet despite these purported functions of male sociality in chimpanzees, explicit tests of the functional significance of cooperation, and the relationship between cooperation, competition, and social structure, are rare. Additionally, male reproductive strategies in chimpanzees have generated considerable controversy. In this dissertation I present research on several communities of eastern chimpanzees in Gombe National Park, Tanzania, a project begun by Jane Goodall in 1960 that continues to the present (Goodall, 1986; Wilson, 2012). I utilize an extensive long-term database of behavioral, demographic, and genetic data to investigate the ultimate function of cooperation in male chimpanzees, the nature and proximate causes of an unprecedented community fission, and the genetic consequences of coercive male reproductive tactics. In this introductory chapter I will review patterns of competition and cooperation in chimpanzees in relation to social structure and summarize the remaining chapters of this dissertation.

1.1 Relationships between males: competition and cooperation

1.1.1 Competition between males

As in most mammals, chimpanzee females invest more resources in offspring than do males. Therefore, the rate of potential reproduction is higher in males than in females, leading to a male-biased operational sex ratio (the ratio of reproductively active males to reproductively active females) and thus competition among males for access to females (Clutton-Brock & Parker, 1992; Mitani, Gros-Louis, & Richards, 1996; Trivers, 1972; see Chapter 3 for historical data on operational sex ratios in Gombe). Because of this, females compete primarily for access to food resources while males compete primarily

for access to mates (Pusey & Schroepfer-Walker, 2013; van Hooff & van Schaik, 1994; Wrangham, 1979).

Male chimpanzees display a number of sexually-selected traits that suggest high levels of male-male competition, including sexual dimorphism, an indicator of pre-copulatory competition, and large testes, which facilitate post-copulatory sperm competition (Andersson, 1994; Peter M. Kappeler & van Schaik, 2004; Møller, 1988). Pre-copulatory male-male competition is frequent and often intense, and results in the establishment of dyadic dominance relationships between community members. The collective set of all dominance relationships in a community is termed the “dominance hierarchy”. Among male chimpanzees, these hierarchies are usually linear, and agonistic interactions can lead to reversals in the hierarchy (Boesch & Boesch-Achermann, 2000; Foerster et al., 2016; Goodall, 1986; Muller, 2002; Newton-Fisher, 2004; Sakamaki & Hayaki, 2015). Hierarchies vary over time and by community from “egalitarian” to “despotic”, depending on the degree to which individuals differ from one another in their likelihood of winning dominance interactions (de Vries, Stevens, & Vervaecke, 2006a; Kaburu & Newton-Fisher, 2015a; van Schaik, 1989).

It has been theorized that dominance relationships between dyads reduce the need for continual aggressive competition (Altmann, 1962; Drews, 1993). However, in chimpanzees several lines of evidence suggest that the costs of competition between males are particularly high. Rates of aggression towards other males are higher among higher-ranking males, and remain high even during periods of hierarchy stability (Boesch & Boesch-Achermann, 2000; Muller, 2002; Muller & Mitani, 2005; Muller &

Wrangham, 2004a). This increased aggression was associated with increased levels of stress hormones in males of the Kanyawara community of Kibale National Park, Uganda, suggesting a proximate energetic cost to dominance competition (Muller & Wrangham, 2004b). In some extreme cases male-male competition can even result in intra-community killings (Kaburu, Inoue, & Newton-Fisher, 2013).

Given the costs of male dominance competition, one would expect significant benefits associated with high rank. Indeed, reproductive success is often correlated with high rank among male chimpanzees (Boesch, Kohou, Néné, & Vigilant, 2006; Feldblum et al., 2014; Newton-Fisher, Emery Thompson, Reynolds, Boesch, & Vigilant, 2010; Wroblewski et al., 2009; Chapter 2). However, siring success is not monopolized entirely by the alpha male.

Models of mating skew predict incomplete monopolization of reproductive success by the alpha male under most circumstances. The “priority of access” model posits that because males cannot usually monopolize mating access to more than one female at once, the degree of reproductive skew is determined by the number of male competitors and the number of synchronously receptive females (Altmann, 1962; Dunbar, 1988). In chimpanzees, patterns of reproductive skew generally follow the predictions of the priority of access model (Boesch et al., 2006; Newton-Fisher et al., 2010; Wroblewski et al., 2009), although low-ranking males are more successful than expected, and young males in particular tend to sire offspring more than would be predicted by this model (Feldblum et al., 2014; Wroblewski et al., 2009; Chapter 2).

Deviation from the strict predictions of the priority of access model is likely the

result of alternative competitive strategies among males, as well as demographic and social factors. Among chimpanzees, high ranking males do not have complete control over mating opportunities (Bray, Pusey, & Gilby, 2016), an effect likely exacerbated as the number of male competitors increases (Alberts, 2003; Alberts, Buchan, & Altmann, 2006; Boesch et al., 2006; Cowlshaw & Dunbar, 1991). Thus, high-ranking males may not always be able to monopolize copulations even with lone estrous females, or may be compelled to allow allies mating access to females in exchange for support (Section 1.1.2 below; Bray et al., 2016; Clutton-Brock, 1998; Duffy, Wrangham, & Silk, 2007). Low-ranking males may also increase their reproductive success via “sneak” copulations, thereby avoiding retaliation by a high-ranking male, or via sperm competition (Wroblewski et al., 2009). Finally, if a male is closely related to a number of females in a group he may sire fewer offspring than expected due to post-copulatory processes (K. K. Walker et al., 2017).

1.1.2 Cooperation and social bonds between males

Despite intense competition, cooperation is frequently observed in male chimpanzees. Kinship plays only a limited role in structuring this cooperation (Goldberg & Wrangham, 1997; Langergraber, Mitani, & Vigilant, 2007; Mitani, Merriwether, & Zhang, 2000; Mitani, Watts, Pepper, & Merriwether, 2002), so that many chimpanzee social relationships involve cooperation between unrelated individuals. For purposes of this introduction, I define cooperation as any act that benefits another individual, regardless of the immediate cost or benefit to the actor (Dugatkin, 1997; Gilby, 2012; van Schaik & Kappeler, 2006). Cooperative behavior among non-kin can be selected for if

the short-term cost of performing the act is offset by either an immediate or delayed benefit. When the benefit to the cooperator is immediate, this is called mutualism, and when the cooperator receives a delayed benefit from the recipient of the cooperative act, this is called contingent reciprocity or exchange (Dugatkin, 1997; Gilby, 2012).

Correlational studies of wild chimpanzees suggest that males exchange contingently a number of different cooperative behaviors, such as coalitionary support (Gomes & Boesch, 2011; Watts, 2002), meat sharing (Mitani & Watts, 2001), and mating opportunities (Bray et al., 2016; Duffy et al., 2007). Most commonly reported as an exchange commodity, however, is grooming. Grooming is frequently exchanged reciprocally within dyads for grooming (Arnold & Whiten, 2003; Gomes & Boesch, 2011; Kaburu & Newton-Fisher, 2015a; Watts, 2002), for agonistic support in within-group aggressive encounters (Kaburu & Newton-Fisher, 2015a; Watts, 2002), and potentially also for support during territorial behavior (Watts & Mitani 2001).

Several recent studies suggest that patterns of cooperative exchange are influenced by the stability or steepness of the male hierarchy. In two communities of eastern chimpanzees that differed primarily in dominance hierarchy steepness, the degree to which male grooming was exchanged for coalitionary support and mating opportunities varied predictably with hierarchy despotism (Kaburu & Newton-Fisher, 2015a, 2015b). Further, in a study of captive chimpanzees, exchange of grooming for support depended on the presence of a clear alpha (Hemelrijk & Ek, 1991). Collectively, these studies suggest that power differentials between individuals influence their relative values as trading partners. This suggests that, in chimpanzees, at least some cooperative

behaviors may be traded according to the rules of a biological market, which applies many of the laws of economic markets to cooperative exchange in non-human animals (Hammerstein & Noe, 2016; Noë & Hammerstein, 1994).

Recently, researchers have noted that traditional models of reciprocal exchange in animal societies are unrealistic. In particular, theoretical and empirical work suggests that cognitive limitations preclude a system of strict tit-for-tat reciprocation because of the tendency to forget or misattribute the behavior of past partners and to discount the value of future benefits (Hammerstein, 2003; Stevens & Hauser, 2004; Stevens, Volstorff, Schooler, & Rieskamp, 2010). Given these cognitive limitations to tit-for-tat cooperation, researchers have proposed that a more likely system for maintaining cooperation is the less cognitively demanding process of emotion-based tracking of relationships, or “emotional bookkeeping” (Aureli & Schaffner, 2002; Aureli & Whiten, 2003; McElreath et al., 2003; Schino & Aureli, 2009). This mechanism may result in the differentiated social relationships often observed among social animals. Relationships thus maintained, which are characterized by friendly and equitable interactions of diverse type and are both strong and stable over time, are termed “social bonds” (Ostner & Schülke, 2014; Silk, Cheney, & Seyfarth, 2013). These bonds may facilitate and be maintained by the exchange of cooperative behaviors (Schino & Aureli, 2009). Recent evidence for an emotional bookkeeping mechanism underlying social bonds comes from a study of hormonal responses to grooming, in which levels of urinary oxytocin increased after grooming bouts between individuals with strong social bonds, but not after grooming bouts between non-bonded individuals (Crockford et al., 2013).

Importantly, most examples of cooperative exchange in the wild seem to take the form of nearly cost-free acts such as grooming, top-down coalitions (*sensu* Chapais, 1995), food sharing, and tolerance (Schino & Aureli, 2009; Watts, 2002, but see Boesch & Boesch-Achermann, 2000). Thus, these acts could serve primarily to maintain social bonds rather than represent a costly tradable commodity (Schino & Aureli, 2009). Yet whether chimpanzees cooperate to receive reciprocated favors, or whether they cooperate to build and maintain social bonds, remains uncertain. Tests of the fitness effects of social bonds and cooperative exchange are needed to better understand the function of cooperation in chimpanzees.

1.1.3 Studies of male relationships in this dissertation

In Chapter 2 I present an investigation of the functional effects of social bonds, agonistic support, and individual grooming effort (often interchanged for support or tolerance) among Gombe males. In this study, I contrasted three hypotheses: the *social bonds* hypothesis, which states that individuals invest selectively in long-term social bonds, which facilitate increased fitness; the *indirect ties* hypothesis, which states that individuals leverage their position in the networks of relationships or coalition formation to increase their fitness; and the *grooming exchange* hypothesis, which states that individuals strategically exchange grooming for tolerance or support from others, which affords them increased fitness. This is the first test of the fitness correlates of social bonds in males of a male philopatric primate species, and the first effort to contrast the functional effects of bond formation and cooperative exchange.

Chapter 3 describes the relationship between male affiliative behavior and the

events preceding a particularly striking example of between-group competition in Gombe. During a five-year period beginning in 1973, members of the original study community separated into two distinct communities, and the members of one were observed or suspected to have killed off the male members of the other. Contemporary observers believed that the initial division represented the fission of a cohesive community, although some wondered if the original study community was actually two separate communities, brought together by provisioning (Bygott, 1974; Goodall, 1986; Goodall et al., 1979). Using association and grooming data from before the division and recent techniques from the field of social network analysis, we first tested whether the division of the original Gombe study community indeed represented the fission of a discrete community. We then investigated whether pre-division association patterns predicted post-division group membership, and potential catalysts of the division. This project sheds light on the factors that influence community cohesion, as well as how male affiliation influences group choice during permanent community division. More generally, it illuminates areas of tension between cooperation and competition in chimpanzee society.

1.2 Male-female sexual conflict

In addition to engendering male mate competition, differential parental investment means that male and female reproductive interests often fail to align, resulting in sexual conflict (Clutton-Brock & Parker, 1992; Trivers, 1972). In most sexually reproducing species, including chimpanzees, males benefit by maximizing their mating opportunities, leading them to compete with each other for access to females. Females

benefit in turn by choosing to mate with the “best” males. As described in the previous section, competition among chimpanzee males for mates is intense and complex, but the extent to which females exercise mate choice has proven controversial.

More recently, researchers have identified sexual coercion as the third pillar of sexual selection (Clutton-Brock & Parker, 1995; Smuts & Smuts, 1993). Sexual coercion is the use of aggression or threat of aggression, often by males, to overcome mate choice by the opposite sex and increase the aggressor’s likelihood of reproduction with the victim (Smuts & Smuts, 1993). This can be direct, when males use aggression to coerce a female into mating, and indirect, when a male uses aggression to prevent a female from mating with other males. Further, this coercion can operate *immediately*, as in forced copulation (e.g. orangutans, *Pongo pygmaeus*: Galdikas, 1985) or *delayed*, as a pattern of long-term intimidation that causes a female to alter her behavior. The definition of sexual coercion contains a behavioral (aggression) and a functional (reproductive success) component, so coercion cannot be identified by observing only the immediate behavior of aggressor and target (Smuts & Smuts, 1993). Thus coercion is often overlooked and likely under-reported, as short-term observation could lead to the mistaken conclusion that the observed distribution of mating behavior represents female choice.

Yet despite the difficulty of studying this phenomenon, sexual coercion has now been reported in a number of species, including weevils (*Euscepes postfasciatus*: Sato & Kohama, 2007), dolphins (*Tursiops spp.*: Sargeant, Watson-Capps, Scott, Connor, & Mann, 2005), mouse lemurs (*Microcebus murinus*: Eberle & Kappeler, 2004), hamadryas

baboons (*Papio hamadryas*: Swedell & Schreier, 2009), mountain gorillas (*Gorilla beringei*: Robbins, 2009), and chimpanzees (Muller, Kahlenberg, Emery Thompson, & Wrangham, 2007). Chimpanzees are an ideal model species to investigate coercion because they exhibit morphologies and behaviors thought to increase sexual conflict and favor coercion, including sexual dimorphism, a promiscuous mating system, high levels of male competition and clear dominance hierarchies, and low female reproductive rates and thus a high incentive for female choosiness (Goodall, 1986). Male chimpanzee aggression against females is well-documented (Goodall, 1986; Muller, 2002; Muller, Emery Thompson, Kahlenberg, & Wrangham, 2011; Muller et al., 2007; Stumpf & Boesch, 2010), but whether this aggression functions as sexual coercion remained equivocal until recently, both within and between subspecies.

Three criteria must be satisfied for aggressive behavior to be considered sexual coercion (Muller, Kahlenberg, & Wrangham, 2009b; Smuts & Smuts, 1993): (1) male-female aggression must increase in reproductive contexts; (2) male-female aggression must correlate with increased male reproductive success; and (3) male-female aggression must impose a cost on the female. Studies testing the sexual coercion hypothesis in chimpanzees have relied on both mating patterns and patterns of female proceptivity (female-initiated sexual behavior) and resistance to male mating efforts (Muller et al., 2011, 2007; Pieta, 2008; Stumpf & Boesch, 2006, 2010). However, proceptivity and resistance by females have been criticized as unreliable indicators of female choice, because both could be influenced by the possibility of reprisal from an aggressive male (Muller, Kahlenberg, & Wrangham, 2009a). Further, measuring resistance is problematic

because an initially resistant female could later mate with a soliciting male. Finally, as will be seen in Chapter 4, sexual coercion appears to function in a delayed manner in chimpanzees. Thus in the following discussion I focus on evidence of delayed coercion from studies of mating patterns and genetic paternity.

In a pair of studies, Muller and colleagues found support for the sexual coercion hypothesis in the Kayawara community of eastern chimpanzees in Kibale National Park, Uganda (Muller et al., 2011, 2007). In these studies: (1) aggression increased in reproductive contexts, when females were swollen and sexually receptive; (2) males that were more aggressive towards females during females' entire ovarian cycle (swollen and non-swollen periods pooled) mated more often with those females when females were most fertile (a period of about four days within a female's estrus period known as the *peri-ovulatory period*, or POP; Muller et al., 2011); and (3) parous females, who received more aggression from males (presumably because males favored them) showed higher levels of cortisol, indicating a significant cost of male aggression (Muller et al., 2007). Notably, the authors found no correlation between male-female aggression *during POP* and mating frequency during POP within dyads (Muller et al., 2011). Thus although males displayed increased levels of aggression towards estrous females, this behavior was *not* correlated with increased mating success when females were most likely to conceive, suggesting that in this population *immediate* coercion is ineffective. Only a long-term pattern of male aggression against females was consistent with successful constraint of female choice during the POP, evidence of *delayed* coercion.

Contradicting these results, Stumpf and Boesch (2010) did not find evidence that

male aggression constrained female mate choice in a western chimpanzee population in Taï National Park, Côte d'Ivoire. In this study; (1) male-female aggression rates did not increase during female estrous periods (in POP or non-POP periods) compared to non-estrous periods; and (2) no significant correlation was found between aggression during estrus or overall (estrous and non-estrous periods pooled) and copulation rates.

Unfortunately, this study did not take male rank into account when considering the effect of aggression on copulation (see Chapter 4), although this could be due to the small number of males in their study communities.

Thus in the two most comprehensive efforts to test the sexual coercion hypothesis, strong evidence supporting *delayed* coercion was found in a larger eastern chimpanzee population (Muller et al., 2011), and no support was found for *immediate* or *delayed* coercion in a smaller western chimpanzee population (Stumpf & Boesch, 2010).

1.2.1 Studies of sexual conflict in this dissertation

In Chapter 4, I present the results of a study of the efficacy of sexual coercion in the Kasekela community of Gombe National Park, Tanzania. This study improves upon previous work in two important ways. First, for the first time we tested for the efficacy of male aggression in constraining female choice using genetically-determined paternity, a direct measure of reproductive success (Muller & Mitani, 2005; Smuts & Smuts, 1993). We also analyzed data within discrete “reproductive windows”, allowing us to determine a more direct association between male-female behavioral interactions and male mating and reproductive success. This project represents the first test of the genetic consequences of male-female aggression in social mammals.

2. The adaptive value of male relationships in the chimpanzees of Gombe National Park, Tanzania

2.1 Introduction

Humans live in large multi-level social groups (Hill et al., 2011), and social relationships have a profound effect on fitness for both males and females (Holt-Lunstad, Smith, & Layton, 2010). While the scale of human cooperation may be unique (Fehr & Fischbacher, 2003; Hill, Barton, & Hurtado, 2009), many other animals are known to form differentiated social relationships (e.g. bats: Wilkinson, 1985; cetaceans: Connor et al., 2001; carnivores: de Villiers et al., 2003; birds: Emery et al., 2007; ungulates: Cameron et al., 2009; primates: Mitani, 2009; Berghänel et al., 2011) and cooperate with other members of their group (Dugatkin, 1997). Nonetheless, the proximate mechanisms by which cooperation impacts fitness in animal social groups remain controversial. Animal social relationships could constitute selective long-term investments (or “social bonds”) or be primarily opportunistic and transactional (Noë & Hammerstein, 1994; Silk, 2007). Few studies have directly contrasted these competing hypotheses.

Animal social relationships are considered to be social bonds when they are characterized by friendly and equitable interactions of diverse type, and are both strong and stable over time (Ostner & Schülke, 2014; Silk et al., 2013). Critically, this means that any measure of social bonds should index several types of affiliative behaviors (Silk et al., 2013). Recent research on non-human animals has found increasing evidence that social bonds are correlated with components of fitness, particularly for females. For example, the strength of a female’s social bonds is correlated with reproductive success

in dolphins (*Tursiops sp.*; Frère et al., 2010) and wild horses (*Equus caballus*: Cameron et al., 2009). In primates, a number of studies of female cercopithecine species have revealed connections between social bond strength (or grooming relationships) and longevity, reproductive success, and offspring survival (yellow baboons, *Papio cynocephalus*: Silk et al., 2003; Archie et al., 2014; chacma baboons, *Papio ursinus*: Silk et al., 2009, 2010; rhesus macaques, *Macaca mulatta*: Brent et al., 2013), although most female-female bonds in baboons appear to exist between close kin.

Bonds between male primates are expected to be less common because in most species adult males are immigrants and not closely related to male group mates. Further, males compete for mating opportunities, and paternities cannot be shared (van Hooff & van Schaik, 1994). Nevertheless, friendly bonds have been identified in males of two macaque species in which males disperse at sexual maturity (Assamese macaques, *Macaca assamensis*: Schülke et al., 2010; Barbary macaques, *Macaca sylvanus*: Berghänel et al., 2011), as well as in two species with female-biased dispersal (chimpanzees: Mitani, 2009; Guinea baboons, *Papio papio*: Patzelt et al., 2014). In these species, preferred social partners are more likely than non-bonded pairs to engage in various forms of cooperative behavior, including grooming and coalitionary support in aggressive conflicts (Berghänel et al., 2011; Mitani, 2009; Schülke et al., 2010). In Assamese macaques the strength of a male's top three bonds was associated with correlates of improved fitness (Schülke et al., 2010). Additionally, in rhesus macaques, measures of grooming and proximity (behaviors often used to identify social bonds) were also associated with improved fitness in males (Brent et al., 2013). These results suggest

that individuals invest selectively in long-term social bonds, which facilitate increased fitness, which we call the *social bonds* hypothesis.

In addition to direct social bonds, individuals may benefit from indirect ties with group members, both via extended coalition networks and extended association networks. Measures of indirect ties take into account not just those individuals with whom an animal interacts directly, but also partners of their social partners (Brent, 2015). Indirect connections were correlated with rank acquisition in male long-tailed manakins, *Chiroxiphia linearis* (McDonald, 2007), survival in juvenile male dolphins (Stanton & Mann, 2012), and reproductive success in both male and female rhesus macaques (Brent et al., 2013). In male chimpanzees, betweenness centrality in the network of aggressive coalition formation was positively associated with rank increase and reproductive success (Gilby, Brent, et al., 2013). These results suggest that individuals may leverage their position in the networks of relationships or coalition formation to increase their fitness, which we call the *indirect ties* hypothesis.

A third possibility is that cooperative exchange may influence male fitness and account for observed patterns of cooperative behavior. While social bonds in non-human primates are often thought to represent long-term investments that facilitate low-cost exchange of cooperative acts within a select subset of dyads (Kummer, 1978), some researchers have suggested that social bonds are unimportant in primate societies, and that instead cooperative behaviors are exchanged according to the rules of a biological market among members of a social group (Barrett & Henzi, 2002; Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Henzi & Barrett, 2002; Noë & Hammerstein, 1994).

According to this view, social bonds are incidental to the more meaningful strategic exchange of cooperative behaviors, such as the exchange of grooming for coalitionary support (Seyfarth, 1977) or grooming for infant handling (Henzi and Barrett, 2002, 2007; but see Silk et al., 2009). In previous studies, correlated rates of cooperative behaviors between chimpanzees suggest the existence of reciprocal exchange (Mitani and Watts, 2001; Watts, 2002; Gomes and Boesch, 2011; but see Gilby, 2006) but the dynamics of reciprocal exchange have not yet been determined. The *grooming exchange* hypothesis states that individuals strategically exchange grooming for tolerance or support from others, which affords them increased fitness.

Because they exhibit flexibility in cooperative strategies, cooperate in a range of contexts, and form strong and enduring social bonds, chimpanzees are an ideal model system for investigating the adaptive value of social relationships (Kaburu & Newton-Fisher, 2015a; Langergraber et al., 2007; Mitani, 2009; Mitani et al., 2000).

Chimpanzees live in permanent social groups, called communities, in which males are philopatric and consequently often more closely related to each other than are females (Inoue, Inoue-Murayama, Vigilant, Takenaka, & Nishida, 2008), although this is not always the case (Lukas, Reynolds, Boesch, & Vigilant, 2005; Vigilant, Hofreiter, Siedel, & Boesch, 2001). Males compete with each other for high rank, which is associated with greater reproductive success (Boesch et al., 2006; Wroblewski et al., 2009). Yet the prevalence of cooperative behaviors in chimpanzees suggests that these behaviors likely aid males in their competition with other members of the community (Muller & Mitani, 2005). Still, no research has investigated the connection between fitness and social

bonds, indirect affiliative ties, or grooming exchange in chimpanzees, or tested these hypotheses against each other.

We investigated the association between social relationships and two correlates of fitness in male chimpanzees: increase in rank, which, because rank predicts reproduction, can be thought of as an investment in future reproductive success (Gilby, Brent, et al., 2013; Wroblewski et al., 2009), and reproductive success measured by paternity. We constructed measures of social connectedness and calculated measures of indirect connections in the networks of social bonds and coalition formation. The *social bonds* and *indirect ties* hypotheses predict that measures of social connectedness or indirect social ties will be positively correlated with rank and reproductive success. We also constructed measures of individual grooming effort with all males, irrespective of the strength or equitability of their overall relationship. The *grooming exchange* hypothesis predicts a relationship between grooming effort, particularly time spent grooming other males, and fitness correlates.

2.2 Methods

2.2.1 Study site and data

Gombe National Park is located in western Tanzania on the eastern shore of Lake Tanganyika. Since 1973, local field assistants have conducted daily full-day focal follows on individuals in the Kasekela community, one of three chimpanzee (*Pan troglodytes schweinfurthii*) communities in the park (Goodall, 1986). Field assistants record the association patterns, social behavior, and location of a focal individual and all other individuals present, and since 1994, collect fecal samples for genetic paternity

analysis (Constable, Ashley, Goodall, & Pusey, 2001). We used behavioral and genetic data from 1990 to 2011 to investigate the fitness consequences of male relationships, subdividing the study period into 11 2-year windows for analysis. However, because data on male aggression are currently digitized from 1994 onward, analyses presented below that include coalition data exclude the first two windows. We included all males in a given period if they were 12 years old at the start of the period and still alive at the end (Feldblum et al., 2014), as males begin to enter the male dominance hierarchy, participate in intergroup encounters, mate with adult females and sire offspring at that age (Goodall, 1986; Wilson et al., 2014; Wroblewski et al., 2009). The community averaged 11.3 such males across periods and 49.3 individuals overall.

To generate measures of dyadic social bonds and individual social connectedness, we began by calculating dyadic indices of association, grooming rate, and grooming equitability. Within each period, association patterns were measured by joint first arrivals in groups of 4 or fewer individuals into focal parties (Murray, Eberly, & Pusey, 2006; Williams et al., 2002). This was used as a proxy for social preference, because male gregariousness (Gilby & Wrangham, 2008; Wrangham & Smuts, 1980) made it impossible to generate differentiated association measures using time spent together. The association index was defined as:

$$\frac{Ar_{AB}}{Ar_A + Ar_B - Ar_{AB}}$$

where Ar_{AB} is the count of joint arrivals of individuals A and B in groups of 4 or fewer, Ar_A is the count of individual A's total arrivals in groups of 4 or fewer, and Ar_B is the

same count for individual B.

We calculated an index of dyadic grooming rate by dividing time spent grooming by the total time both individuals were in a group together and one was focal. Until 1997, field assistants recorded grooming using scans at 5-minute intervals. After 1997, grooming was extracted from long-hand notes, and to calculate grooming indices we used only those bouts with recorded start and end times.

Because relationships must be both strong and equitable to be considered social bonds, for each dyad, we calculated Silk et al.'s (2006) index of grooming equitability (equivalent to the equitability index from Mitani 2009), which ranges from 0 to 1, with 0 being entirely unequal and 1 being entirely equal. This measure is defined as:

$$1 - \left| \frac{g_a \rightarrow g_b}{g_a \leftrightarrow g_b} - \frac{g_b \rightarrow g_a}{g_a \leftrightarrow g_b} \right|$$

where $g_a \rightarrow g_b$ is the time individual a spends grooming individual b , $g_b \rightarrow g_a$ is the time individual b spends grooming individual a , and $g_a \leftrightarrow g_b$ is the total time a and b spent grooming.

We then calculated dyadic composite sociality indices (“CSIs”) following previous studies (Silk et al., 2009, 2006). We divided the association, grooming rate, and grooming equitability indices by their averages in each period then averaged among them as follows:

$$\frac{\left(\frac{AI_{ijp}}{\overline{AI}_p} + \frac{GI_{ijp}}{\overline{GI}_p} + \frac{EI_{ijp}}{\overline{EI}_p} \right)}{3}$$

where AI_{ijp} is the association index between individuals i and j in period p , \overline{AI}_p is the

average association index value in period p , GI_{ijp} is the grooming index between individuals i and j in period p , \overline{GI}_p is the average grooming index value in period p , EI_{ijp} is the equitability index between individuals i and j in period p , and \overline{EI}_p is the average equitability index value in period p .

Using the set of dyadic CSIs, we calculated two measures of individual social connectedness and used these two measures as predictors in our analyses. First, we created a summary measure of each individual male's direct social relationships by summing the top 3 CSIs for each individual in each period. This metric quantifies bonds in a manner that is unaffected by longitudinal changes in group size (Schülke et al., 2010; Silk et al., 2009, 2006). Second, as a measure of indirect connectedness, we calculated individual betweenness centrality in the network of dyadic CSIs using the igraph package in R (Csárdi and Nepusz, 2006; R Core Team, 2016). Betweenness measures the number of shortest paths (known as geodesics) between other nodes in a network that connect through a particular node, or roughly the propensity for an individual to connect those that aren't themselves connected (Freeman, 1979). In the case of a weighted network in which edge weights indicate tie strength, distances between nodes are calculated as the sum of the inverse of edge weights, and betweenness is calculated using these re-weighted geodesics. Betweenness measures were then normalized to account for community size in each period, and then Z transformed to account for variation in overall sociality in different periods.

We extracted instances of coalitionary aggression from detailed narrative field notes. Aggression events were instances of directed displays, chases, or contact

aggression, and were considered coalitionary if two or three males directed aggression at one or more males (Gilby, Brent, et al., 2013). Coalitions of three males were scored as three dyadic coalitions. We determined an index of coalition frequency by dividing number of coalitions formed by the time both individuals were observed together in each period. We then calculated betweenness centrality in the network of coalition indices, as this measure was found to be associated with rank change and reproductive success in male chimpanzees in Gombe (Gilby, Brent, et al., 2013).

Finally, we created measures of grooming given and grooming received for each male in each period. This was calculated both as the total time spent grooming others and total time being groomed, and as a rate by dividing by the sum of the time an individual and his potential grooming partners were both present in a group together when one was the focal individual. We then Z-transformed these measures within each period to account for variation in sociality from period to period.

Much of the work on the connection between social integration and fitness in humans (Holt-Lunstad et al., 2010; House, Landis, & Umberson, 1988; Seeman, 1996; Smith & Christakis, 2008) and cercopithecines (Archie et al., 2014; Silk et al., 2010) has focused on longevity. However, while 50% of Gombe males alive at age 12 years (the age of sexual maturity in Gombe; Wroblewski et al., 2009), survive to age 29, the mean age of males who sire offspring at Gombe is 21.4 years, and only about 10% of genotyped offspring were sired by males over age 30 (Figure 1; Gombe Stream Research Centre, unpublished data). Thus longevity likely plays less of a role in male fitness than it does in females, and we focus instead on rank change and reproductive success as

correlates of fitness more relevant to male chimpanzees.

Dominance rank scores were generated from records of submissive pant-grunt vocalizations. To measure rank change, we calculated the difference between male rank at the beginning and end of each period using a modified Elo score method, with parameters optimized using maximum likelihood fitting (Foerster et al., 2016). This method dynamically updates rank scores at each interaction, allowing for the calculation of rank on a given date.

To measure rank *during* each two year period for the reproductive success analysis, we used the modified David's score (MDS) method, which uses matrices of interaction data to generate rank scores for individuals over defined windows (de Vries, Stevens, & Vervaecke, 2006b). Because this measure is influenced by changes to group size, we standardized MDS scores within each period by Z-transformation.

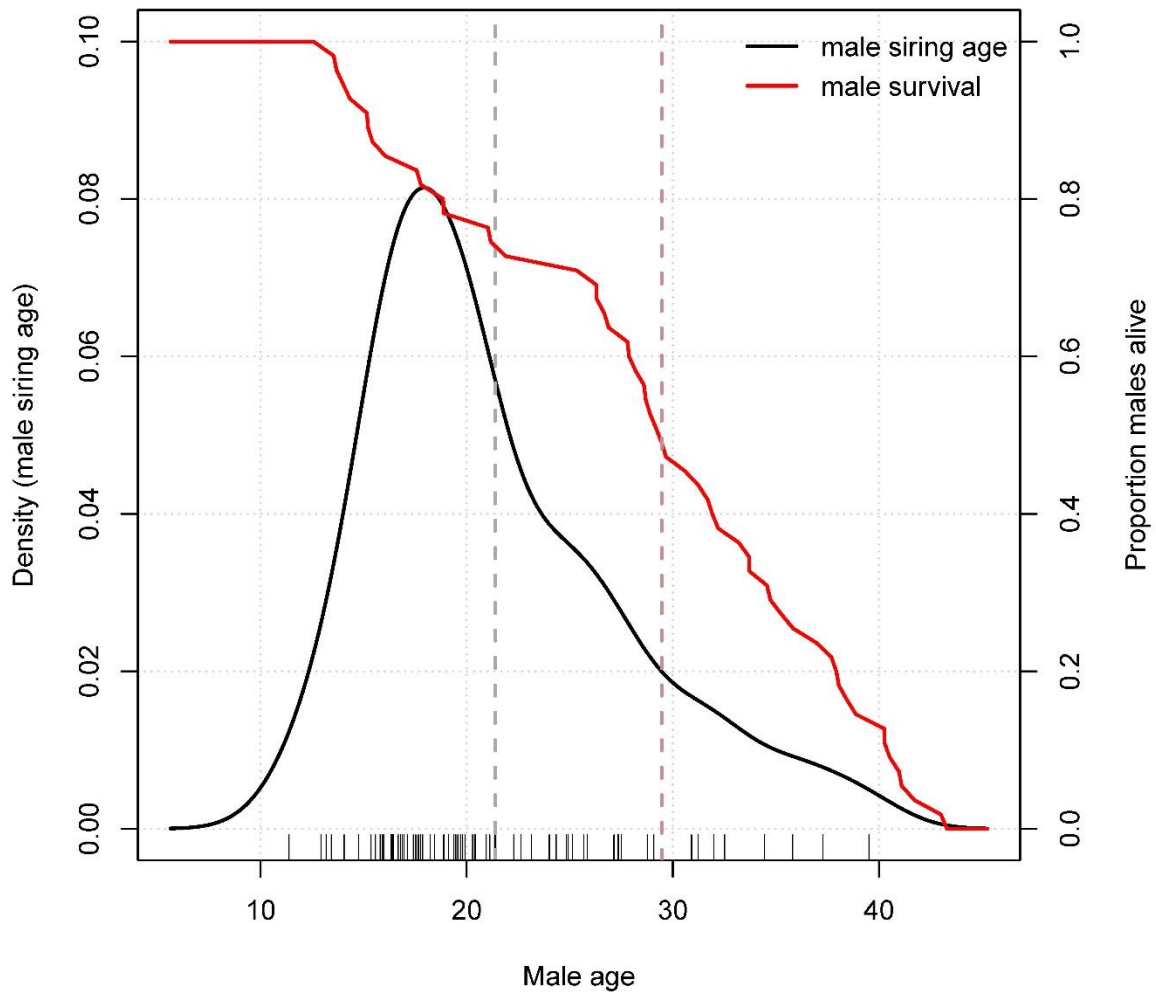


Figure 1: Age of male sires vs. male survival.

The black line presents the distribution of the age of the sires of genotyped offspring in Gombe National Park (N = 74). The grey dotted vertical line represents the mean value of male sires (21.4 years). The red line represents the survival curve for males who survived at least to age 12 (and therefore represents the pool of males that reached reproductive maturity), and the red dotted vertical line represents the point at which 50% of males remain alive (29.0 years).

Because individuals likely vary in their value as potential bond partners (de Waal, 1982; Seyfarth, 1977; Watts, 2010), we created four measures of the rank and relatedness of each individual's top bond partners. We generated pairwise relatedness values using

Queller and Goodnight's R (Queller & Goodnight, 1989) calculated from DNA extracted from fecal sampling (K. K. Walker et al., 2017; Wroblewski et al., 2009), and then for each male we generated a measure of 1) the average relatedness among his top 3 partners, and 2) the highest relatedness value among his top 3 partners. We also created measures of the average MDS among each male's top 3 partners, as well as the highest MDS score in that set.

Further, changes to the male hierarchy, and to the alpha male's security at the top of the hierarchy, are associated with changes in bond formation and patterns of cooperative exchange (Gilby & Wrangham, 2008; Hemelrijk & Ek, 1991). Thus, we calculated despotism ratio (Feldblum et al., 2014; Chapter 4), a measure of hierarchy steepness in each period, by dividing the MDS value of the highest ranking male by the MDS value of the second highest.

Males in the Kasekela community tend to reach their highest ordinal rank at an average age of 21.5 years, (Feldblum, unpublished data), and begin to lose their condition and ability to recover from setbacks in dominance competition around age 30 (Goodall, 1986). Thus we expected age to have a non-linear association with male competitiveness. We classified males in our analyses as *young* (12-19 at the start of a period), *prime* (20-29), and *old* (30 and above) (Goodall, 1986).

We used 44 paternity assignments from DNA extracted from non-invasive fecal samples using a microsatellite-based exclusion method (described in more detail in Chapter 4 and Wroblewski et al., 2009). For infants with known paternity, to determine the period in which each siring event took place we used likely siring dates inferred from

female swelling records or, in the absence of swelling records, by subtracting 226 days from the infant's birthdate (Boehm & Pusey, 2013). We excluded one known paternity because the sire died before the end of the period and one because the sire was less than 12 years old. All paternity assignments from the current analysis were reported in earlier publications (Constable et al., 2001; Feldblum et al., 2014; Gilby, Brent, et al., 2013; K. K. Walker et al., 2017; Wroblewski et al., 2009).

2.2.2 Rank change analyses

To examine the effects of male sociality on rank change, we ran linear mixed models with rank change as the dependent variable, and measures of sociality, Z-transformed Elo score at the start of the period, and age category as fixed effects, and male identity as a random effect. We removed one male from these analyses, because he dropped in rank more than twice as far as any other male in the sample, although results do not change substantively if the data point is included.

Our analyses proceeded in three steps to avoid problems with statistical power. First, we ran a set of "CSI-only" models to determine whether the influence of direct male bonds on rank change might be mediated by the rank or relatedness of bond partners or by the steepness of the male hierarchy. In these models, we included the measures of the rank and relatedness of each male's top 3 partners, as well as despotism ratio, as interaction terms with the CSI measure. These models did not include measures of indirect connectedness or grooming effort. We then used a model selection algorithm with corrected AIC (AICc) as our selection criterion (Burnham, Anderson, & Huyvaert, 2010) in the MuMIn package in R (Bartoń, 2015) to determine whether any of the

interaction terms were found in the set of best models ($\Delta\text{AICc} \leq 2$), and those terms were then included in future full models.

In the second step, we repeated the analysis, adding betweenness centrality in the networks of dyadic CSIs and measures of grooming given and grooming received. We again used multi-model inference with AICc as our selection criterion, and considered the models within two points of the best model to have strong support. We used model averaging to determine the parameter estimates for those terms appearing in the best models (Burnham & Anderson, 1998).

In the third and final step, we repeated the analyses from step 2 but added a measure of betweenness in the network of coalition formation. This round of analysis was undertaken separately because we lacked data on coalitionary aggression from 1990 through 1993, and thus the models were fit using a smaller dataset.

2.2.3 Reproductive success analyses

To investigate the factors influencing reproductive success, we ran a set of generalized linear mixed models with siring success (siring one or more offspring during a given period) as a logistic response variable. We included measures of sociality, Z-transformed MDS score, and age category as main effects. We also included the total number of offspring sired by all males in the period as a main effect to account for differences in the number of reproductively cycling females between periods, and male identity as a random effect. We removed two individuals from the data set, as both were likely sterile during the study period as the result of testicular wounds.

As in the analysis of rank change, we initially ran a set of CSI-only models

including measures of the rank and relatedness of each male's top 3 partners, as well as the despotism ratio, as interaction terms with the CSI measure. We again employed multi-model inference to select the interaction terms that appeared in any of the best models ($\Delta AICc \leq 2$) for inclusion in the next set of analyses.

After addressing potential mediating factors, we repeated the analysis including betweenness centrality in the network of dyadic CSIs and measures of grooming given and received. Finally, we conducted a third round of analysis using the reduced dataset that included betweenness in the coalitions network. We again employed multi-model inference with AICc as our selection criterion, and considered models within two points of the best model to have significant support. We finally determined the model averaged parameter estimates for the terms appearing in the best models.

2.3 Results

2.3.1 Rank Change analyses

In the initial CSI-only step, the only interaction term to appear in a set of best models was the measure of the highest relatedness among an individual's top 3 partners. However, because of strong evidence of multicollinearity (GVIF = 15.7; Fox and Monette, 1992), we removed the relatedness term and re-ran the model selection procedure. In these best models, summed CSI and starting Elo score were important predictors of rank change (Table 1). Males with high summed CSI values tended to increase in rank, while males with low summed CSI values tended to fall in rank (Figure 2).

Table 1: The best “CSI-only” model for predicting rank change

List of models within two AICc points of the best model (only one in this case), as well as the model averaged estimates from the list of all models. “CSI” is the summed CSI measure, and “Elo beg” is the measure of Z-transformed Elo score at the start of a period.

Model	intercept	CSI	Elo beg	Δ AICc	Akaike weight
1	-214.3	50.0	-125.6	0.00	1.00
se (best mod)	81.6	16.1	21.4		
avg (all mods)	-201.5	48.7	-121.9		
se (all mods)	91.0	18.0	23.3		

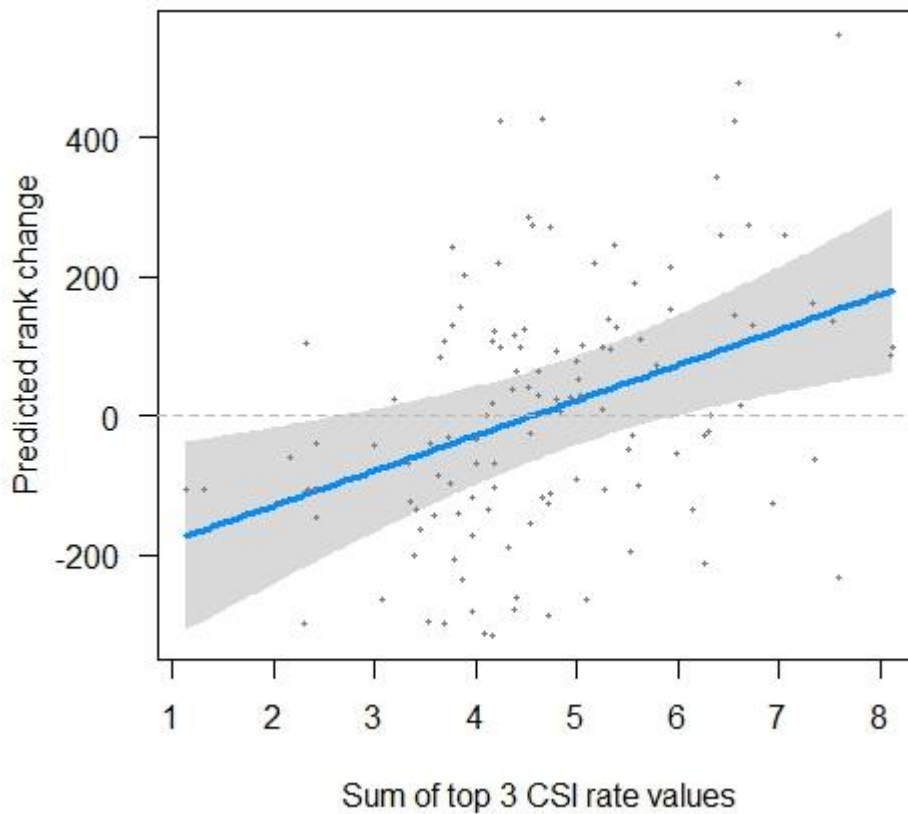


Figure 2: Predicted rank change (over a two-year period) vs. sociality (as measured by summed CSI values) for all males. Points are partial residuals

In the second analysis step, which included all sociality factors, we found age, starting Elo score, grooming received, grooming given, the interaction between starting

Elo and both grooming given and received to be important factors in predicting rank change, while CSI did not appear in any of the best models (Table 2). Males who received high rates of grooming rose in rank, although this effect was particularly pronounced among already high-ranking males (Figure 3). Males who groomed others at high rates increased in rank if they were low-ranking, but fell in rank if they were high-ranking (Figure 4). Using the conservative model-averaged parameter estimates, low ranking males that groomed others at a high rate (Elo and grooming measures 2 standard deviations below and above the mean, respectively) were predicted to rise 320 Elo points. Because the average difference in Elo score between individuals of adjacent rank during the study period was 102, an increase in Elo score of 320 on average corresponded to a three-position rise in ordinal rank.

We found weaker support for the importance of summed CSI (Table 2), as this measure was only present in two of five best models. Results were substantively unchanged whether grooming effort and CSI were calculated using rates of or time engaging in their component behaviors (Table 9 in Appendix A).

Table 2: The best models predicting rank change

The list of models within 2 AICc points of the best model for predicting rank change (full data set; no coalitions). “age: prime” and “age: old” represent the effects of being a *prime* and *old* male, respectively, relative to being a *young* male. “betw CSI” represents the effect of betweenness in the network of dyadic CSIs, “CSI” is the summed CSI measure, “Elo beg” is the measure of Z-transformed Elo score at the start of a period, “Grm IN rate” and “Grm OUT rate” are rates of grooming others and being groomed, and “Elo beg: Grm IN rate” and “Elo beg: Grm OUT rate” are the interactions between Elo score at the start of a period and grooming rates.

model	intercept	age: prime	age: old	betw CSI	CSI	Elo beg	Grm IN rate	Grm OUT rate	Elo beg: Grm IN rate	Elo beg: Grm OUT rate	Δ AICc	Akaike weight
1	87.47	+	+			-101.39	104.55	-27.19	45.32	-88.37	0.00	0.32
2	107.99	+	+			-97.90	112.11	-33.22		-49.67	0.73	0.22
3	-51.60	+	+		27.80	-104.03	84.96	-46.37	47.78	-90.64	0.89	0.20
4	99.64	+	+	-132.68		-99.17	103.22	-29.78	48.47	-93.05	1.77	0.13
5	-13.59	+	+		24.50	-100.06	95.21	-50.41		-49.82	1.95	0.12
avg (best mods)	52.96	-103.04	-107.94	-17.56	8.65	-100.70	100.92	-35.60	30.70	-76.20		
se (best)	98.21	41.43	53.49	77.15	18.38	21.76	35.39	29.41	31.07	31.67		
avg (all mods)	15.08	-77.66	-81.63	13.36	-28.26	-107.42	87.32	-29.20	29.19	-70.38		
se (all)	124.46	57.30	65.94	22.29	102.92	25.08	43.55	34.21	33.31	38.05		

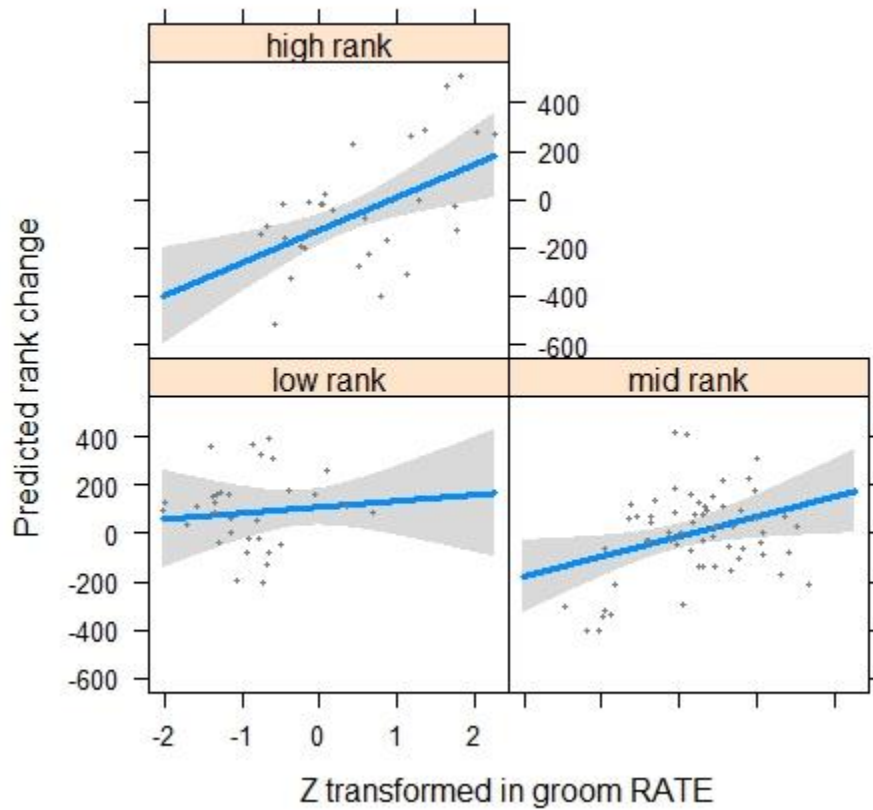


Figure 3: Predicted rank change over a two year period (with confidence regions) vs. rate of received grooming, for males of low, middle, and high rank. Points are partial residuals.

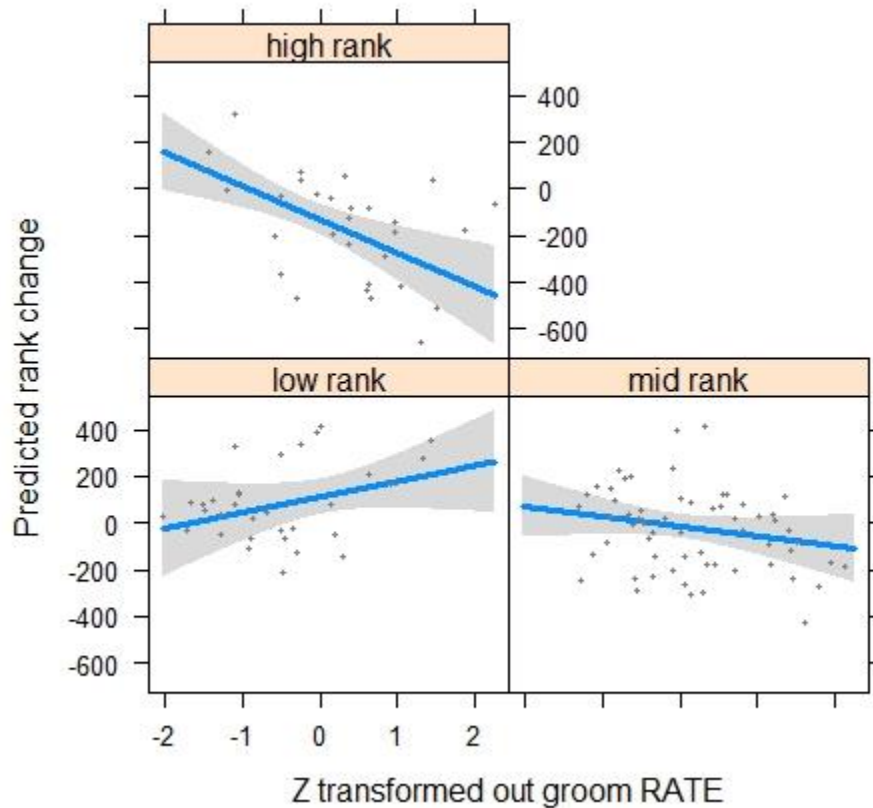


Figure 4: Predicted rank change over a two year period (with confidence regions) vs. rate of received grooming, for males of low, middle, and high rank. Points are partial residuals

When including coalitionary betweenness, despite the smaller dataset in this step of the analysis, we again found age, starting Elo score, grooming received, grooming given, and the interaction between starting Elo and both grooming received and given to be important factors in predicting rank change (

Table 10 in Appendix A). The associations between these factors and rank change were similar to those in the previous round of analyses, though slightly attenuated in each case. As with the previous step, summed CSI was not an important predictor of rank change. Additionally, in these models, betweenness in the network of coalition

formation was an important predictor of rank change, such that males with higher coalitionary betweenness tended to rise in rank (Figure 5). Using the model-averaged parameter estimates, males with high betweenness in the coalitions network (2 standard deviations above the mean betweenness score) were predicted to rise between one and two ordinal rank positions.

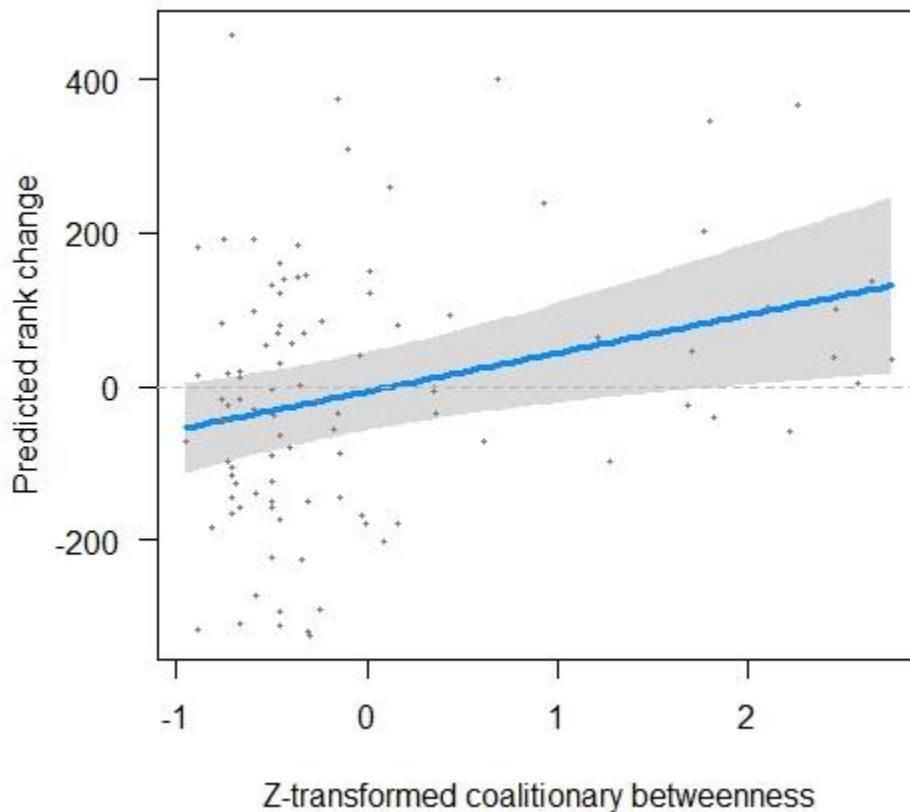


Figure 5: Predicted rank change vs. betweenness in the network of coalition formation. Points are partial residuals.

2.3.2 Reproductive Success analyses

In the initial CSI-only models, the measure of the highest relatedness among an individual's top 3 partners was again the only interaction term to appear in a set of best

models. However, again based on strong evidence of multicollinearity (GVIF = 17.5), we removed the relatedness term and repeated the model selection procedure. In the set of best CSI-only models excluding interaction terms, age, rank, and total offspring sired during a period were important predictors of siring success, but summed CSI was not. Males were more likely to sire offspring if they were young and if they were high ranking, and during periods where more conceptions occurred (Table 3). In later steps we included no first order interactions with the summed CSI measure.

Table 3: Factors predicting reproductive success in “CSI-only” models.

The set of best models, and model-averaged estimates of the factors predicting reproductive success from the initial “CSI-only” round of model selection. “age: prime” and “age: old”: the effect of *prime* and *old* age categories, respectively, on rank change relative to the *young* category. “CSI”: the summed CSI measure, “total sired”: the total number of offspring of known paternity sired in a given period, “MDS”: Z-transformed modified David’s score.

Model	age: prime	age: old	CSI	total sired	MDS	ΔAIC_c	Akaike weight
1	+	+		0.31	0.47	0.00	0.18
2	+	+			0.48	0.45	0.14
3						0.54	0.14
4				0.26		0.61	0.13
5				0.27	0.34	0.80	0.12
6					0.33	0.80	0.12
7	+	+		0.31		1.22	0.10
8	+	+				1.77	0.07
avg (best mods)	-0.53	-0.29		0.15	0.23		
se (best)	0.66	0.61		0.20	0.28		
avg (all mods)	-0.55	-0.31	0.02	0.15	0.23		
se (all)	0.67	0.63	0.13	0.20	0.29		

In the second and third steps, none of CSI, coalitionary betweenness, or CSI betweenness appeared in the sets of best models (Table 4, Table 11, Appendix A).

Instead, we found that in addition to age, rank, and total offspring sired, grooming received, grooming given, and the interaction between rank and grooming given were important predictors of siring success. We also found limited support for the importance of the interaction between grooming received and rank (Table 4, Table 11, Appendix A). Males were more likely to sire offspring if they were young and high ranking. Males with high rates of grooming others were more likely to sire offspring, an effect most pronounced for low and mid-ranking males (Figure 6). On the other hand, males were less likely to sire offspring if they received more grooming (Figure 7), although this effect, too, may be more pronounced for low and middle-ranking males (Table 11 in Appendix A).

Because summed CSI values were correlated with rank change, and rank improvement may be a correlate of future reproductive success, we ran a final set of models to investigate whether CSI or rank change in one period predicted reproductive success in the next. However, none of the model terms of interest predicted future reproductive success.

Table 4: The best models for predicting reproductive success

Models within 2 AICc points of the best model for predicting reproductive success (full data set; no coalitions) and effect sizes. “age: prime” and “age: old”: effects of *prime* and *old* age categories, respectively, relative to *young* age category. “CSI”: the summed CSI measure, “Grm IN rate” and “Grm OUT rate”: rates of grooming others and being groomed, “MDS”: Z-transformed modified David’s Score in each period, “Elo beg: Grm IN rate” and “Elo beg: Grm OUT rate”: interactions between Elo score at the start of a period and grooming rates. Effect sizes are multiplicative effects on likelihood of siring at least one offspring of a one unit change in the variable. Values above 1 will increase likelihood of siring offspring.

Model	age: prime	age: old	CSI	tot sired	Grm IN rate	Grm OUT rate	MDS	MDS: Grm IN rate	MDS: Grm OUT rate	ΔAICc	weight
1				1.35	0.25	2.54	2.20			0.00	0.19
2					0.25	2.52	2.19			0.62	0.14
3				1.35	0.24	2.93	2.37		0.74	0.80	0.13
4	+	+		1.34	0.31	3.41	2.50		0.63	0.90	0.12
5	+	+			0.28	3.48	2.59		0.64	1.09	0.11
6					0.24	2.88	2.35		0.74	1.38	0.09
7	+	+			0.26	2.84	2.43			1.71	0.08
8	+	+		1.32	0.29	2.73	2.33			1.80	0.08
9			1.23	1.35	0.22	2.20	2.11			1.93	0.07
avg (best mods)	0.66	0.99	1.01	1.19	0.26	2.81	2.33		0.84		
se(best mods)	1.94	1.75	1.11	1.23	1.69	1.54	1.39		1.30		
avg (all mods)	0.64	0.92	1.07	1.18	0.33	2.17	2.03	1.01	0.85		
se(all mods)	1.99	1.83	1.26	1.23	1.99	1.80	1.50	1.19	1.33		

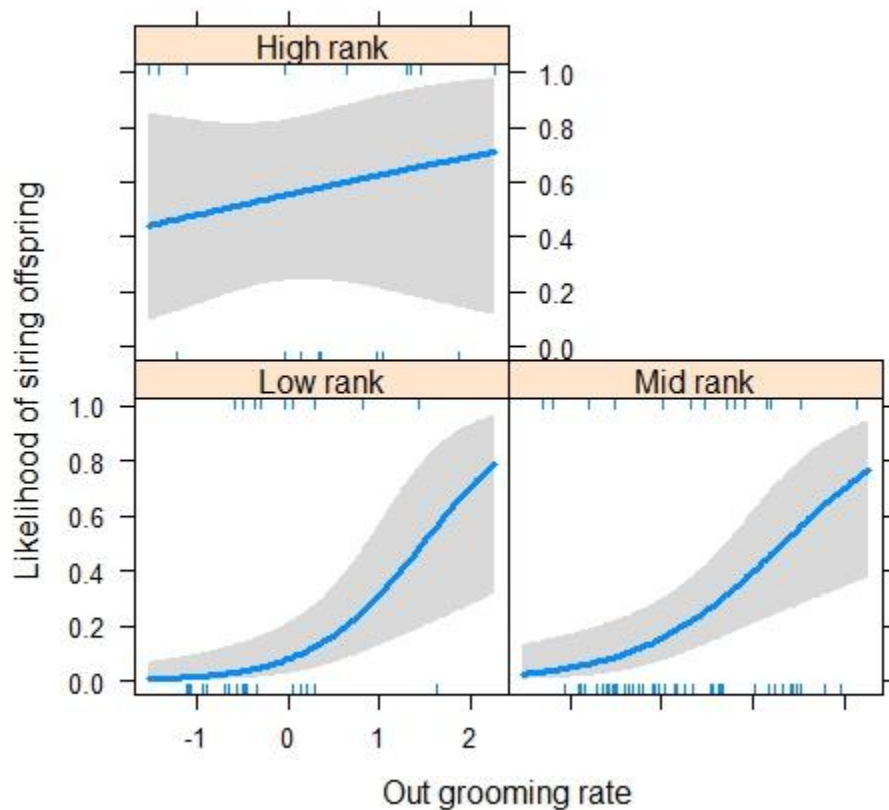


Figure 6: Predicted likelihood of siring offspring vs. rate of grooming others at three levels of male rank

“Low rank” = 1.25 standard deviations below mean rank, “mid rank” = mean rank, and “high rank” = 1.25 standard deviations above mean rank. Tick marks along x axes indicate individual male grooming rates at each rank level, with marks along the top of each plot indicating males that successfully sired offspring, and those along the bottom unsuccessful males.

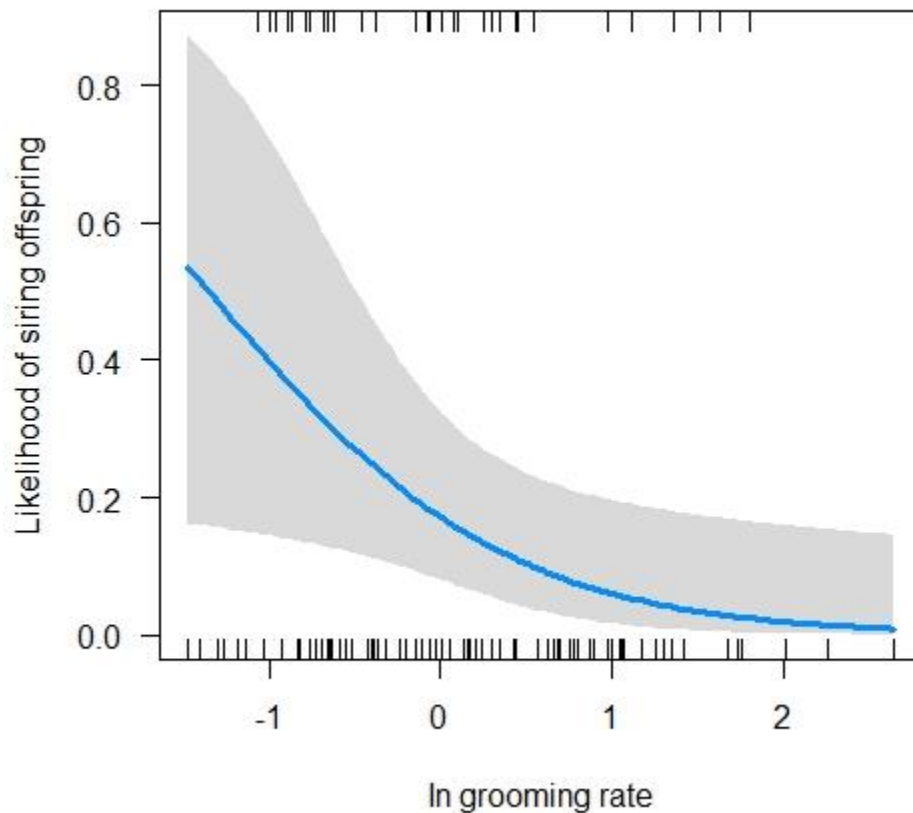


Figure 7: Predicted likelihood of siring offspring vs. rate of received grooming

Tick marks along x axes indicate individual male grooming rates at each rank level, with marks along the top of each plot indicating males that successfully sired offspring, and those along the bottom unsuccessful males. Results not separated by rank because the interaction between received grooming and rank was not an important predictor of siring offspring.

2.4 Discussion

We found only weak support for the hypothesis that social bonds promote fitness in male chimpanzees. The summed CSI measure was not associated with rank change except in the initial set of rank change models that did not include other measures of sociality and in three of the 12 best models in the frequency-based analysis. Further, we found no evidence that social bonds are associated with male reproductive success, as the

summed CSI measure never appeared in any of the sets of best models predicting siring success.

We also found no evidence to support the hypothesis that indirect affiliative ties are positively associated with male fitness. The CSI betweenness measure was present in one of the best models predicting rank change, but with a negative rather than positive effect. Further, this measure did not appear in any of the best models predicting reproductive success. However, as found in previous work in Gombe (Gilby, Brent, et al., 2013), betweenness in the network of coalition formation was positively associated with rank change, although this effect did not extend to reproductive success in the current analysis.

The differing evidence for the association between the CSI and coalitionary betweenness measures may be explained by the fact that network analysis is only appropriate for studying a particular system if something is flowing through the network. Information flows readily through human networks, allowing individuals to benefit from indirect ties (Wasserman & Faust, 1994), but in the absence of language information cannot propagate through an extended chimpanzee social network. Thus, perhaps it is unsurprising that indirect connections in the network of CSIs do not improve fitness. However, individuals with high coalitionary betweenness may be able to leverage their positions as potential coalition partners to two other individuals in conflict for rank and reproductive benefits (de Waal, 1982; Nishida, 1983; Watts, 2010). A similar effect is also observed in human organizational settings (Burt, 2009).

In contrast to the tenuous association between social bonds and fitness measures,

we found robust evidence of an association between grooming effort and both male rank change and reproductive success, although in some cases this association was mediated by rank. Low ranking males who groomed others at a high rate, or for long durations, rose in rank and had an increased likelihood of siring offspring. For high-ranking males, grooming others at high rates was associated with a decrease in rank but was not strongly associated with reproductive success.

This result is consistent with earlier models of grooming in primates (Seyfarth, 1977) and empirical results in chimpanzees (Kaburu & Newton-Fisher, 2015a; Watts, 2000, 2002) suggesting that low-ranking males groom others for tolerance or support, which may translate into rank increases and mating opportunities (Bray et al., 2016; Duffy et al., 2007). For high-ranking males, grooming others may be counterproductive, or may be a strategy employed by males who are falling in the hierarchy for other reasons. Additionally, high-ranking males may be less likely to groom others for access to females.

On the other hand, although rates of received grooming were positively correlated with rank change particularly in high-ranking males, received grooming was negatively associated with likelihood of siring offspring for all males. While these results resist easy interpretation, perhaps males that are rising in rank (and receive more grooming) are seen as potential threats by high-ranking males, and are thus actively excluded from mating opportunities. However, a more detailed analysis is needed to investigate this possibility.

Indeed, follow-up work is needed to determine whether male grooming patterns lead to rank change and reproductive outcomes, or whether the results presented here

result from confounds. In particular, an analysis incorporating both grooming effort and grooming partner choice may allow for a more concrete interpretation of the results presented here.

The dearth of evidence for the effect of male social bonds on reproductive success that we report could be due to insufficient data, sex differences in the value of bonds across primates, species differences in the value of bonds between cercopithecines and chimpanzees, or fitness effects of social bonds manifesting in ways not considered in the present analysis. Further research on female chimpanzees is needed to address the possibilities of species and sex differences in the fitness values of social bonds. Additionally, although one study of the fitness correlates of animal social bonds has addressed reproductive rate (Cameron et al., 2009), most evidence comes from studies of individual survival or infant survival (Archie et al., 2014; Frère et al., 2010; Silk et al., 2009, 2010, 2003; Yee et al., 2008). A connection between chimpanzee social bonds and health is suggested by recent findings that individuals that interact with bond partners rather than non-bond partners show reduced levels of urinary glucocorticoids in a range of contexts (Wittig et al., 2016). Further, in humans, the fitness effects of social integration are thought to arise via social interactions and perceived support that promote healthy behaviors and reduce stress (Cohen, Gottleib, & Underwood, 2000). Thus future studies in chimpanzees should investigate whether social bonds enhance male and female health and longevity.

The results presented here may help explain the finding that kinship plays a limited role in cooperation in chimpanzees (Goldberg & Wrangham, 1997; Langergraber

et al., 2007; Mitani et al., 2000). Some males may benefit from strong bonds with closely-related group members, but it may be more common for males to engage in strategic cooperative exchange with unrelated males. Another possibility is that social bonds may benefit males by facilitating cooperative range defense (Pusey, 1979; Sugiyama, 2004). In Gombe larger ranges are associated with greater food availability and shorter inter-birth intervals (Williams et al., 2004). But because the spoils of territorial expansion represent a public good, if the primary function of bonds is to facilitate territorial behavior differential social integration would not translate to differential reproductive success.

If future research also finds weak support for a connection between social bonds and longevity in male chimpanzees, and between social bonds and both reproductive success and longevity in female chimpanzees, it would suggest that the strong association between social bonds and fitness in humans (Hill et al., 2009; Holt-Lunstad et al., 2010) represents a derived trait rather than a modification of a chimpanzee-like social pattern.

3. Social network analysis reveals the timing and causes of a unique chimpanzee community fission: Gombe's Four Years' War

3.1 Introduction

Researchers have long understood that animals experience both costs and benefits from living in groups, and that group sizes represent a balance between these competing forces. Individuals in larger groups tend to experience greater within-group competition for resources, including mates, but may be buffered against between-group competition, predation and infanticide (Alexander, 1974; Kummer, 1971; van Schaik & Kappeler, 1997; Wrangham, 1979). In particular, in territorial species, larger groups are more effective in increasing their range (arboreal ants, *Azteca trigona*: Adams, 1990; rattling cisticola, *Cisticola chiniana*: Carlson, 1986; chimpanzees, *Pan troglodytes schweinfurthii*: Goodall, 1986; Nishida, 1968; lions, *Panthera leo*: Grinnell, Packer, & Pusey, 1995; Mosser & Packer, 2009; baboons, *Papio cynocephalus*: Markham, Alberts, & Altmann, 2012; spider monkeys, *Ateles chamek*: Wallace, 2008).

When the costs of within-group competition (Darwin, 1871; Gillespie & Chapman, 2001; Janson & van Schaik, 1988; Trivers, 1972; Wrangham, Gittleman, & Chapman, 1993) or of maintaining relationships or spatial cohesion (Barrett, Henzi, & Rendall, 2007; Dunbar, 1992; Johnson, 1982) exceed the benefits of group membership, fissions can occur. Indeed, group fissions are observed in many mammalian species (white-nosed coatis, *Nasua narica*: Gompper, Gittleman, & Wayne, 1997; spotted hyenas, *Crocuta crocuta*: Holekamp, Ogutu, Dublin, & Smale, 1993; prairie dogs,

Cynomys ludovicianus: Manno, Dobson, Hoogland, & Foltz, 2007; brown bats, *Eptesicus fuscus*: Metheny, Kalcounis-Rueppell, Bondo, & Brigham, 2008; lions: Pusey & Packer, 1987; VanderWaal, Mosser, & Packer, 2009; Cape ground squirrels, *Xerus inauris*: Waterman, 2006; reviewed in Storz, 1999), and are particularly well-documented in female-philopatric cercopithecine primates. In these species, fissions are often observed when groups become large or have an imbalanced sex ratio (macaques, *Macaca sp.*: Furuya, 1968; baboons, *Papio sp.*: Nash, 1976; Van Horn, Buchan, Altmann, & Alberts, 2007), or after a period of hierarchy instability (macaques: Koyama, 1970; baboons: Nash, 1976). Fissions usually occur along matriline (macaques: Chepko-Sade & Olivier, 1979; Chepko-Sade & Sade, 1979; Cheverud, Buettner-Janusch, & Sade, 1978; Dittus, 1988; Kuester & Paul, 1997; Ménard & Vallet, 1993; Okamoto & Matsumura, 2001; Widdig et al., 2006; baboons: Van Horn et al., 2007), although not always (macaques: Chepko-Sade & Olivier, 1979; Widdig et al., 2006; baboons: Collins, Sindimwo, & Goodall, 2006). For example, females may sometimes abandon kin during fissions to avoid overly large daughter groups (Van Horn et al., 2007). Fissions in these species can be associated with violence (e.g. Nash, 1976), but if observed, it is rarely lethal. Instead, members of recently-fissioned cercopithecine groups are sometimes observed associating peacefully with each other (macaques: Missakian, 1973; geladas, *Theropithecus gelada*: Snyder-Mackler et al., 2012).

In human groups, fissions are also often associated with large group size. This may be due to the difficulties of maintaining or keeping track of relationships as group size increases, a phenomenon known as “scalar stress” (Johnson, 1982). Although

humans may mitigate the limiting influence of scalar stress on group size through several linguistically- and culturally-mediated mechanisms (Dunbar, 1993; Friesen, 1999; Johnson, 1982; Moffett, 2013), permanent group fissions are nevertheless extensively documented (Yanomamo: Chagnon, 1975; Hunley, Spence, & Merriwether, 2008; Smouse, Vitzthum, & Neel, 1981; Semi Senoi: Fix, 1975; Hutterites: Mange, 1964; Olsen, 1987; Xavante: Neel & Salzano, 1967; reviewed in: Walker & Hill, 2014). In pre-industrial human groups, fissions are often preceded by a struggle for leadership or “headmanship”, and usually occur along kinship lines (Chagnon, 1975; Fix, 1975; Mange, 1964; Neel, 1967; Neel & Salzano, 1967; Smouse et al., 1981; R. S. Walker & Hill, 2014). Leadership struggles and non-random assortment may also be hallmarks of group fissions in agrarian and post-industrial societies (Hurd, 1983; Olsen, 1987; Zachary, 1977).

In contrast to humans and female-philopatric cercopithecine primates, only four apparent permanent fissions have been documented in wild male-philopatric primate groups. This may be because male philopatry is sometimes associated with cooperative range defense (Pusey, 1979), which increases the benefits of membership in larger groups (Wrangham, 1979). An uncertain case was reported in bonobos (*Pan paniscus*) (Kano, 1992), and two clearer cases in muriquis (*Brachyteles arachnoides*), neither of which is aggressively territorial (Strier, 1990; Wilson et al., 2014). In muriquis, the fissions appeared to be initiated by peripheral females, with males following and experiencing a more favorable sex ratio in the splinter group (Strier, Boubli, Possamai, & Mendes, 2006; Strier, Mendes, Rímoli, & Rímoli, 1993; Tokuda et al., 2013). In the fourth case,

researchers observed an apparent fission of a group of chimpanzees in Gombe National Park in 1973, followed by the formation of two distinct daughter communities, “Kasekela” and “Kahama” (Goodall, 1986).

Permanent community fission would seem particularly unlikely in chimpanzees given the importance of group size in chimpanzee territorial behavior. Chimpanzees live in large multi-male, multi-female communities with a median size of 46 individuals (Wrangham et al., 2006), although communities can number nearly 200 individuals (Sandel, Reddy, & Mitani, 2016). They live in fission-fusion societies, forming temporary and fluid subgroups, or “parties” (Goodall, 1986). Occasionally, large parties of males (sometimes also including females) conduct cooperative boundary patrols at the edge of their community range, and sometimes make excursions into the territory of neighboring communities (Goodall, 1986; Mitani & Watts, 2005). In such instances, encounters with members of a rival community can result in lethal attacks (Watts & Mitani, 2001; Wilson et al., 2014), and the best predictor of lethal aggression in intergroup encounters is imbalance in party size (Manson & Wrangham, 1991; Wrangham, 1999).

Because this pattern of territorial behavior is unusually violent among primates (Manson & Wrangham, 1991), and because male numbers are so important in territorial encounters, the consequences of fission in chimpanzees should be particularly severe. Indeed, from 1974 to 1977, researchers at Gombe observed a series of territorial incursions and attacks by Kasekela males resulting in the death or disappearance of five Kahama males and one female. By 1977, all seven males and one female of the Kahama

community had disappeared, in what became known as the “Four-Year War” (Goodall, 1986).

The origins of the apparent fission of the study community, and subsequent extermination of the Kahama community, remain uncertain, in part because, beginning in 1963, initial observations of the original study community were made at a “feeding station”, where researchers used bananas to habituate, and facilitate observation of, the chimpanzees. There, provisioning led to large aggregations of chimpanzees (Wrangham, 1974), potentially masking differentiated social preferences. Nevertheless, by 1966, researchers recognized that, of the nineteen known mature and adolescent males, some spent more time to the north of the feeding station and some to the south (Goodall, 1986). 1971 saw a gradual decrease in association between males of the two subgroups (Bygott, 1974; Goodall, 1986). During this time, the southern group visited the feeding station less frequently (Wrangham, 1974). By the end of 1972, although northern and southern males continued to interact peacefully elsewhere in the community range, the southern males had stopped visiting the feeding station entirely, and an older male, Hugh, disappeared. In 1973, Kasekela and Kahama were recognized as separate communities.

Many researchers have assumed that these events represent the only community fission ever observed in wild chimpanzees. Nevertheless, some contemporary observers noted that they could not rule out the possibility that provisioning either brought together two distinct communities that eventually re-separated or temporarily arrested a fission that was already in progress (Bygott, 1974; Goodall, 1986; van Lawick-Goodall, 1975). Consistent with this “two communities” hypothesis, in 1971, several southern males were

once observed associating with 3 or 4 unhabituated males (Bygott, 1974). Most evidence, however, supports a “single community” hypothesis. Before the establishment of the feeding station, known males were observed near both the northern and southern boundaries of the park (Goodall, 1965; Van Lawick-Goodall, 1968), and in 1971, researchers observed northern and southern males participating together in cooperative territorial behavior (Bygott, 1974).

Although previous studies describe the events preceding the apparent fission (Bygott, 1974, 1979, Goodall, 1983, 1986; Goodall et al., 1979; van Lawick-Goodall, 1975; Wrangham & Peterson, 1996), none have attempted a quantitative treatment of its patterning and causes. We present a case study using newly-digitized data and recently-developed social network analysis tools to analyze the timing and trajectory of subgrouping patterns prior to the formation of the Kasekela and Kahama communities. This approach facilitates a more direct investigation of potential catalysts of the presumed fission and the relationship between daughter community membership and pre-fission subgroup patterning. Further, the methods we employ can be applied to investigate fissions in other species, as well as social structure more generally.

We built social networks using observations of association and grooming at the feeding station, and determined ranging patterns from chimpanzee focal follows beyond the feeding station. Using these data, we tested the community fission hypothesis against the two communities hypothesis. If the events preceding the Four Years’ War indeed represented a community fission, we expected subgrouping structure to begin to emerge and patterns of subgrouping to become more consistent as the fission approached.

Alternatively, the two communities hypothesis predicts subgrouping structure to have been prevalent and consistent throughout the study period.

Next, we explored the patterning and proximate causes of the presumed fission. We analyzed the relationship between pre-split association patterns and post-split community formation. Using the historical notes from Gombe and descriptions of fissions in other species, we determined a set of potential catalysts which we tested for temporal alignment with changes in subgroup structure. Candidate catalysts were changes in 1) male demography, 2) sex ratio, 3) male dominance hierarchy, and 4) provisioning protocol.

3.2 Methods

Observations began at the feeding station in 1963 (Goodall, 1986; Wilson, 2012). Until February 1968, researchers recorded the order in which individuals arrived at the feeding station each day; individuals arriving together were assigned the same arrival order number. Thereafter, observers recorded direction and time of all arrivals. Observers at the feeding station also recorded all-occurrence grooming at 2-minute intervals. Data from 1967 to 2000 (when provisioning ceased) have been extracted from the original checksheets. Ranging data come from early focal follows beyond the feeding station from 1970 to 1972, during which observers recorded party composition and location at the beginning and end of each follow.

We included males at least 12 years of age at the start of a period in the analyses, as individuals over 12 can participate in intergroup encounters and compete for mating opportunities (Wilson et al., 2014). Thus our data set included 19 males from 1967 to

1972 (for feeding station arrival data), and 16 males from 1970 to 1972 (for grooming and ranging data). Because only three of 25 known females eventually joined the southern Kahama community, all of whom were peripheral, we focus our analyses on males. Initial analysis of subgrouping patterns in female association networks revealed no clear relationship between network structure and any of the factors considered below.

We created 11 networks of dyadic association in six-month periods from September 1967 to 1972 (the first period was only 4 months long). Because, especially before 1969, provisioning resulted in large and long-lasting aggregations of chimpanzees (Wrangham, 1974), networks based on time spent together at the feeding station were too densely connected to allow calculation of meaningful measures of subgrouping. Instead, we measured affiliative tendency using counts of joint first arrivals at the feeding station as a proxy for affiliation elsewhere in the forest (Foerster et al., 2015; Pusey, 1980). Prior to February 1968, we considered two individuals to arrive jointly if they had been assigned the same arrival number by the original observers. Thereafter, we considered two individuals to arrive together if their arrivals occurred within 5 minutes of each other and their directions of arrival were within 45°. The resulting networks of joint first arrivals are weighted and undirected.

We next created six 6-month grooming networks from January 1970 to December 1972 by summing 2-minute grooming scans between males in each interval. The resulting networks are weighted and directed.

Then, we extracted all available pre-fission ranging data from the focal follows conducted between August 1970 and December 1972. Chimpanzee locations during

follows were initially recorded on maps by field observers, and later transposed onto a grid system overlaid on the park map. We used data on the grid coordinates of the start and end points of each follow, recorded for all individuals present during each follow, and georeferenced each grid cell using a map overlay in ArcGIS (ESRI, 2010). Total root mean squared error for the 5 maps used for georeferencing was between 33 and 58 meters in all cases, using at least 10 reference points each. We then determined range centroids for each male in five 6-month intervals from mid-1970 to 1972 by averaging all x and y coordinates from follows in which he was present. We included in the ranging analysis those individuals with at least three recorded ranging coordinates (mean \pm s.d. = 132.5 ± 117 coordinates per individual per interval), which led to the exclusion of one individual in one period.

3.2.1 Subgrouping analyses:

Network subgrouping structure emerges from patterns of social preference over time. To quantify subgrouping in association and grooming networks we used a metric called modularity, which measures the degree to which ties connect individuals in the same subgroup, given a particular set of subgroup assignments. Modularity is defined as the fraction of all network ties (or, in the case of a weighted network, tie *strength*) that connect individuals in the same subgroups minus the fraction expected if network ties were assigned randomly (Newman & Girvan, 2004). Values near 0 indicate a network in which within-subgroup ties are no more dense than if randomly assigned without regard to subgroup, and those approaching 1 indicate a network in which all ties are found within subgroups. Thus one can search for subgroup structure in a network by finding

subgroup assignments that have large modularity scores (Newman, 2006b).

To identify subgroups, we used two algorithms that directly optimize modularity: Newman's leading eigenvector algorithm and the fast greedy algorithm (Clauset, Newman, & Moore, 2004; Newman, 2006a, 2006b). We used the igraph package in R version 3.3.1 (Csárdi & Nepusz, 2006; R Core Team, 2016) with the resolution parameter set to the default value of 1. Because neither algorithm tests every possible division of the network, they are not guaranteed to return subgroups corresponding to the global maximum modularity score (Good, De Montjoye, & Clauset, 2010). Thus, for each network we used both algorithms and chose the subgroup assignment with the higher modularity score. In most periods the two algorithms returned identical subgroups and modularity scores.

3.2.2 Ranging data:

To determine the relationship between ranging and community formation, we created a matrix of Euclidean distances between range centroids for each dyad as our dependent matrix, and a binary matrix indicating whether each dyad ended up in the same community after the fission as our independent matrix, in five 6-month periods from mid-1970 through 1972. We excluded individuals from this analysis who died before the fission occurred.

We used double semi-partialing quadratic assignment procedure (QAP) modelling to determine the relationship between ranging similarity and post-split community co-membership in each period (Dekker, Krackhardt, & Snijders, 2007; Krackhardt, 1988). This procedure uses a permutation approach to determine the likelihood that an

observed correlation between corresponding elements in two (or more) matrices could be observed by chance. It iteratively permutes the rows and columns of the independent matrix and stores the correlation of the permuted and dependent matrix, and then compares the correlation of the original matrices with the distribution of permuted correlations to arrive at a p-value. We ran QAP regressions with 2000 permutations each in UCINET (Borgatti, Everett, & Freeman, 2002).

3.2.3 Modelling community co-membership vs. association and grooming

We used the same QAP modelling procedure to determine the relationship between post-fission community makeup and pre-fission patterns of a) association, and b) grooming in each 6-month period. Again excluding individuals who died before the fission, we used the dyadic association and grooming measures in dependent matrices and binary scores representing community co-membership in independent matrices, although results do not change substantively when switching dependent and independent matrices in these analyses.

The QAP procedure determines whether there is a significantly higher correlation between patterns of association or grooming and post-fission community membership than would be expected *by chance*, whereas the modularity optimizing algorithms attempt to determine the particular subgrouping assignment that maximizes within-group relative to between-group ties. Even if the latter procedures determine that subgrouping structure did not match the Kasekela-Kahama split exactly in a given period, QAP modelling might reveal that there was some association between eventual community membership and pre-split subgrouping patterns.

3.2.4 Identification of potential catalysts

Based on contemporary descriptions of the fission (Bygott, 1974; Goodall, 1983, 1986; Goodall et al., 1979; van Lawick-Goodall, 1975; Wrangham, 1974; Wrangham & Peterson, 1996) and descriptions of fissions in other species (eg. Furuya, 1968; Tokuda et al., 2013), we identified four types of events that could have catalyzed the fission.

First, using demographic records, we identified the death dates of five adult males and nine adult females between 1967 and 1972. We calculated betweenness centrality in the networks of joint arrivals using the *igraph* package in R version 3.3.1 (Csárdi & Nepusz, 2006; R Core Team, 2016) for individuals in each period to determine whether any individual whose death occurred soon before the fission had been particularly central to the social network. Individuals with high betweenness may play a role in maintaining group cohesion in chimpanzees (Kanngiesser, Sueur, Riedl, Grossmann, & Call, 2011).

Next, based on daily records of female sightings and reproductive histories, we calculated two measures of adult sex ratio on the first day of each 6-month period. These were socionomic sex ratio (the ratio of adult males to adult females) and operational sex ratio (the ratio of adult males to adult females that are neither pregnant nor experiencing postpartum amenorrhea). We determined pregnancy windows using the timing of sexual swellings within the plausible bounds of pregnancy length, if observed, or by Gombe-specific average pregnancy length if the female was not observed with a sexual swelling during her conception window (Boehm & Pusey, 2013). Periods of postpartum amenorrhea lasted from parturition to the resumption of full sexual swelling.

Next, we investigated the potential influence of changes in the male hierarchy on

social network structure. Because we lack detailed data on dominance interactions during the study period, we relied on the timing of conspicuous challenges to, and overthrows of, the alpha male based on the descriptions of Bygott (1974) and Goodall (1986). Goliath was alpha when research began in Gombe, but lost his position to Mike in 1964. Humphrey, an eventual Kasekela male, rose to the alpha position in mid-1971. While he could usually intimidate all other males in the study community individually, Humphrey had an uncertain dominance relationship with suspected brothers and eventual Kahama males Charlie and Hugh. Beginning in December 1970, Charlie, sometimes accompanied by Hugh, began to occasionally intimidate Humphrey, and thereafter Humphrey and his two rivals increasingly began to avoid each other (Bygott, 1974).

Finally, we identified changes to the provisioning regimen during the study period. Researchers made three such changes. Beginning in August 1967, chimpanzees were fed bananas from 19 metal and concrete boxes, embedded in the ground and opened remotely using a system of underground wires, and widely spaced to reduce monopolizability. Under this system, chimpanzees were fed on average every other day, although feeding days were scheduled unpredictably. In July 1968, primarily in an effort to reduce aggression at the feeding station, researchers began to feed selected parties of chimpanzees from one box per individual, but only if they had been in the feeding area less than 15 minutes, and were in a group of 6 individuals or fewer. Under this system individuals were generally fed once every 10 days. Finally, in June 1969, researchers began feeding chimpanzees from boxes embedded in a covered trench, which further reduced competition and rates of aggression at the feeding station (Wrangham, 1974).

Although each change was made to reduce the predictability of provisioning, beginning in 1971 researchers fed southern males every time they visited the feeding station in an ultimately fruitless attempt to reverse their declining attendance. The 1967 and 1968 changes were followed by a decline in the number of visitors to the feeding station per day, but attendance remained stable after the final change in 1969 (Wrangham, 1974).

3.3 Results

3.3.1 Subgrouping Analyses

Modularity in the networks of male joint arrivals remained low through 1970, and in 1971 began rising sharply to a high of 0.39 in the first half of 1972 (Figure 8A, Table 5). In the second half of 1972, the last 6-month period before the fission, modularity fell only because a number of eventual Kahama males rarely visited the feeding station during that period ($n = 19$ total arrivals vs. 810 for Kasekela males). Beginning in 1971, subgroup membership began to consistently match post-fission community membership patterns (Figure 9, Table 5). Because modularity remained low until 1971, and because partitions of the earlier data do not agree with the final fission, these results match predictions of the community fission hypothesis, but not the two communities hypothesis.

In male grooming networks, modularity rose to 0.11 in the first half of 1971, and then sharply in the second half of 1971 to 0.4. Unlike the modularity trajectory in the association networks, modularity then fell in the first half of 1972 to the levels approaching those in 1970 (Figure 8A, Table 5). Further, only in the second half of 1971 did subgroup assignment approximate post-fission community membership (with one male more closely aligned with the other subgroup than with his post-fission group

mates) (Table 5). These results do not lend support to either the community fission or two communities hypotheses.

Table 5: Modularity Optimizing Algorithm results

Max Q indicates the maximum of the modularity scores returned by the two modularity optimizing algorithms (Fast-Greedy and Leading Eigenvector Optimization). “Subgroup match?” indicates whether the subgroup assignments returned in the max Q split matched post-fission community membership. * indicates a period during which subgroup membership matched post-fission community membership, with additional males who died prior to the fission in each group (Figure 1c). ** indicates a period during which subgroup membership matched post-fission community membership for all individuals but one.

	1967b	1968a	1968b	1969a	1969b	1970a	1970b	1971a	1971b	1972a	1972b
Arrivals											
Max Q	0.074	0.048	0.11	0.063	0.093	0.11	0.12	0.16	0.27	0.39	0.069
Subgroup match?	N	Y*	N	N	N	N	N	Y	Y	Y	Y
Groom											
Max Q						0.049	0.083	0.11	0.4	0.076	0.064
Subgroup match?						N	N	N	N**	N	N

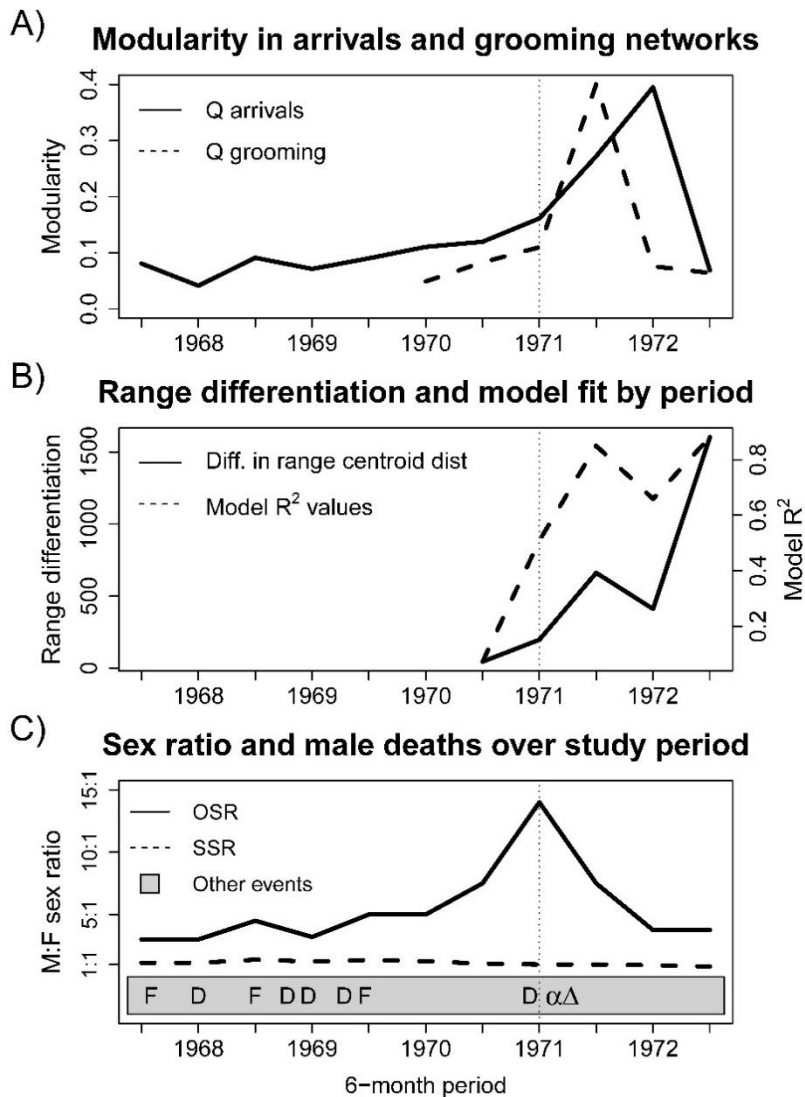


Figure 8: Timelines of modularity, ranging patterns and potential catalysts during the study period.

A) Modularity scores (denoted “Q”) associated with the optimum subgroup assignments as determined by the fast-greedy and leading eigenvector algorithms. B) Average difference in Euclidian distance between range centroids for individuals who ended up in different vs. the same post fission community (plotted on the left-hand y axis) and the fit of QAP models predicting range centroid difference from post-split community co-membership patterns (plotted on the right-hand y axis). C) The timeline of operational sex ratio (OSR), socionomic sex ratio (SSR), changes to the feeding regimen (denoted “F”), male deaths (denoted “D”) and the ascension of new alpha male Humphrey (denoted “ $\alpha\Delta$ ”).

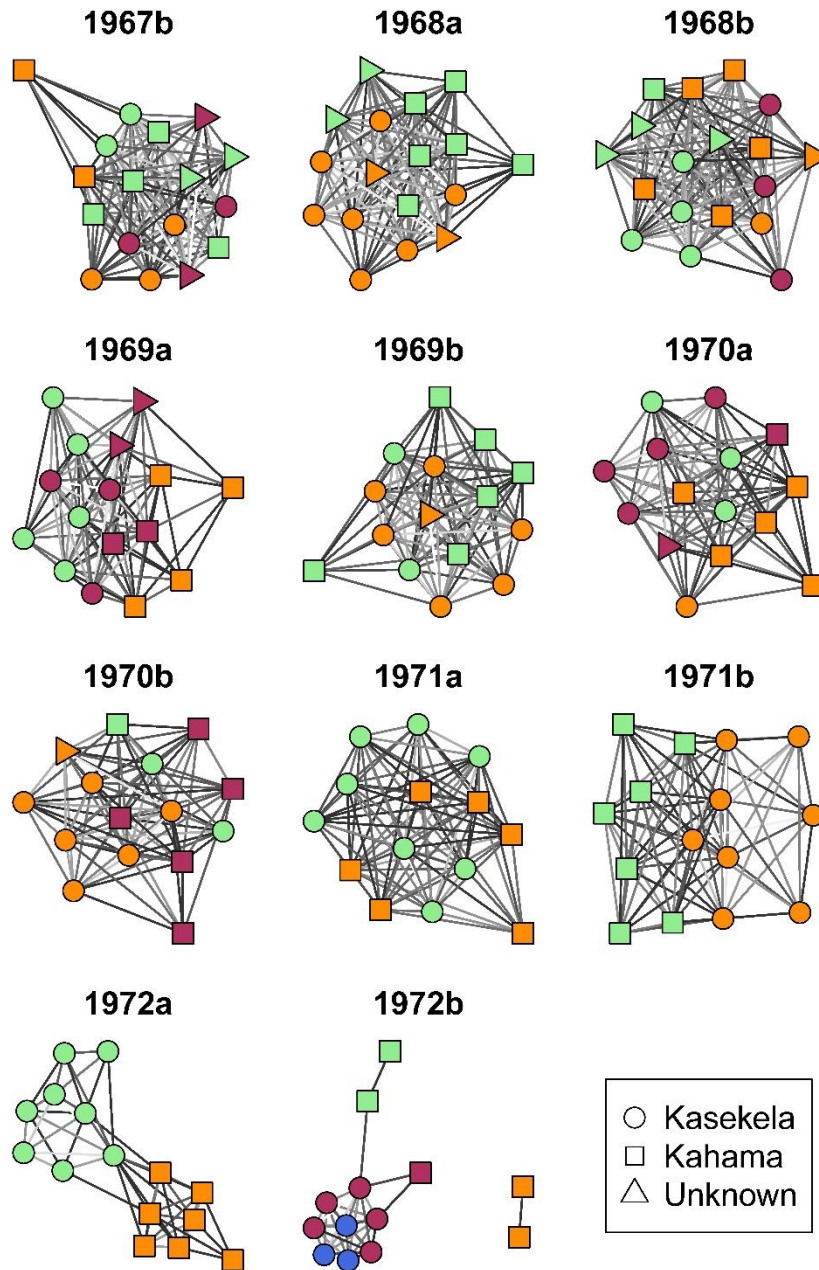


Figure 9: Networks of joint arrivals among males in each 6-month window.

“a” and “b” denote the first and second half of each year (e.g. “1968a” indicates January-June 1968). Node shape indicates each individual’s post-fission community membership (individuals represented as triangles died before the fission, so could not be assigned to Kasekela or Kahama), while node color indicates community assignment based on the modularity optimizing algorithms. Stronger ties are indicated by darker edges.

3.3.2 Ranging

Post-split community co-membership was a significant predictor of distances between range centroids in all 6-month periods, but model fit improved dramatically in 1971 and 1972 compared to 1970 (Table 6). Additionally, individuals who belonged to the same post-split community ranged only slightly closer to each other than to others in 1970, but this effect increased to more than a kilometer and a half by the end of 1972 (Figure 8B, Figure 10, Table 6). Thus the initial slight ranging affinity between eventual post-split community mates was followed by a progressive dissolution of spatial cohesion in the study community, supporting the community fission hypothesis.

Table 6: QAP results

Results and model fit statistics from QAP regressions, with Arrivals, Grooming, and Ranging as dependent variables and post-fission community co-membership as the independent variable. R² is the overall model fit, effect size is the average difference in number of joint arrivals, grooming bouts, or meters between range centroids, respectively, for individuals in the same post-fission community vs. those in different post-fission communities. *p* val. is the probability that the correlation between independent and dependent matrices is observed by chance given the observed distribution of cell values.

	1967	1968	1968	1969	1969	1970	1970	1971	1971	1972	1972
	b	a	b	a	b	a	b	a	b	a	b
Arrivals											
R ²	0.014	0.049	0.067	0.024	0.089	0.091	0.143	0.257	0.406	0.288	0.279
effect size	0.98	2.42	1.49	0.49	2.49	2.78	1.92	3.28	4.27	2.64	6.51
<i>p</i> val.	0.10	0.02	0.01	0.06	0.01	0.003	0.002	0.001	0.001	0.001	0.001
Grooming											
R ²						0	0.004	0.045	0.116	0.044	0.155
effect size						-3.2	2.8	14.7	11.3	20.3	37.1
<i>p</i> val.						0.57	0.19	0.03	0.001	0.006	0.001
Ranging											
R ²							0.073	0.509	0.85	0.659	0.881
effect size (m)							-44.5	-197	-661	-411	-1603
<i>p</i> val.							0.02	0.001	0.001	0.001	0.002

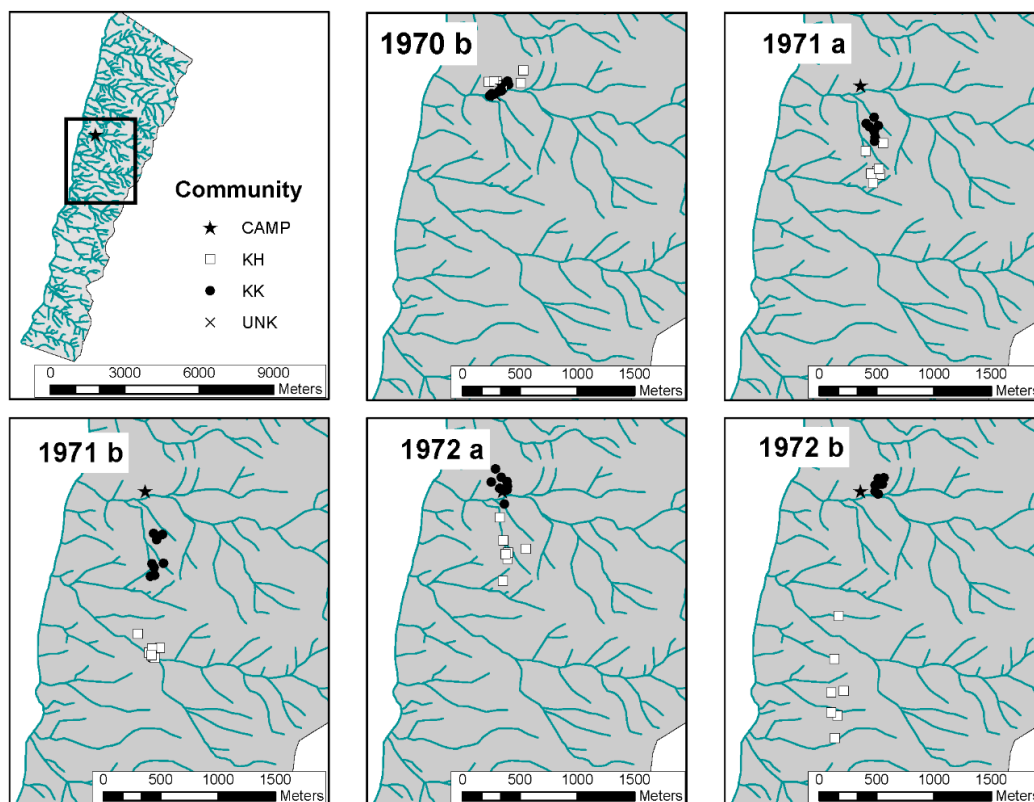


Figure 10: Average male range position in Gombe National Park in the 6-month periods for which we have ranging data.

“Camp” = feeding station, “KK” = eventual Kasekela male, “KH” = eventual Kahama male, “UNK” indicates the male (Leakey) in the ranging dataset who died in October 1970 and thus cannot be assigned to Kasekela or Kahama. Leakey appears only in 1970 b, and his range overlaps with several KK males so his symbol is mostly obscured by the filled circles on the map.

3.3.3 Association patterns and group membership

In a series of QAP regressions, post-split community co-membership was significantly associated with pre-split association matrices in all periods except the second half of 1967 and the first half of 1969, and model fit increased in the periods before the fission (Table 6). With regard to grooming, a series of QAP regressions

revealed that community co-membership was significantly associated with pre-split grooming patterns beginning only in 1971, with model fit and effect sizes increasing dramatically after 1970 (Table 6). These results suggest a relationship between patterns of affiliative behavior and post-fission community in all periods, but one that grows stronger over time, thus providing mixed support for the two hypotheses.

3.3.4 Potential catalysts

Based on the preceding analyses, we conclude that the process of fission most likely began at the beginning of 1971. Three potential catalyst events occurred close to this time, and thus represent plausible causes of the fission. First, the increasing modularity and range differentiation in 1971 followed closely the death of an aging male Leakey (who died of a respiratory infection in October 1970, at the estimated age of 35; Figure 8C). Four other adult males died between January, 1968 and May, 1969, and eight adult females between January 1968 and April 1969, but no individual other than Leakey died within a year of January 1971. However, Leakey had below-average betweenness centrality in the association networks in all of the periods before his death (Table 12, Appendix A), so does not appear to have been particularly influential.

Early 1971 also coincided with the dominance struggle between Humphrey (an eventual Kasekela male) and Charlie and Hugh (eventual Kahama males; Figure 8C). Beginning in December 1970, the relationship between Humphrey and Charlie and Hugh became increasingly tense and avoidant, even when other males were associating peacefully (Bygott, 1974).

The socionomic sex ratio changed little over the course of the study period, but

the operational sex ratio grew to a high of 14:1 in the first half of 1971, although it dropped again by 1972. This peak in operational sex ratio coincided with the onset of increasing modularity (Figure 8C), although it fell again thereafter. But because modularity continued to rise, it is unlikely that operational sex ratio was the sole cause of increased subgrouping before the fission.

Changes to provisioning, however, did not co-occur with the beginning of the fission process in early 1971. The final change in feeding regimen occurred in June 1969 (Wrangham, 1974), a year and a half before the onset of increased modularity in the study community (Figure 8C). Further, if this change led to the dissolution of the community via reduced interest in the feeding station as a food source, one would expect reduced attendance after the change. Instead, aggregation size and duration at the feeding station were slightly higher after the change, and the rate of provisioning of southern males actually increased as the fission approached (Wrangham, 1974). Thus there is no evidence that changes in the provisioning regimen affected the fission, as both timing of changes in provisioning and subsequent changes in aggregation patterns fail to align with changes in subgrouping patterns.

3.4 Discussion

Numerous lines of evidence support the hypothesis that the study group at Gombe was indeed a single community, with incipient subgroups, that began to fission in early 1971. By 1973, the fission was complete. In contrast, we found little evidence to support the two communities hypothesis. Subgrouping and ranging patterns at the beginning of the study period were poor predictors of the eventual community division, but as the

fission approached they aligned more closely with post-fission community membership.

Beginning in 1971, modularity in the arrivals network increased dramatically, falling only in the 6-month period immediately before the fission due to a decline in visits to the feeding station by southern (Kahama) males. Further, beginning in 1971, subgrouping patterns in the arrival networks consistently matched post-split community membership. Modularity in the grooming networks also began increasing in the first half of 1971, reaching a high of 0.26 in the second half of 1971. However, grooming network modularity fell again in the first half of 1972, even though all individuals were observed during that period. Moreover, only in the second half of 1971 did subgroup membership in the grooming networks approximate post-fission membership (with only one male assigned to a subgroup not corresponding to his post-fission community), while in all other periods subgroups contained both eventual Kasekela and Kahama males. We suspect that the patterns of modularity in grooming networks differed from those of arrivals because grooming sometimes functions to reduce or reconcile social conflict in chimpanzees and other primates (de Waal, 2000; McKenna, 1978; Schino, Scucchi, Maestripietri, & Turillazzi, 1988; Terry, 1970; Watts, 2006). As the sub-groups became more distinct and more hostile to each other, a secondary increase in grooming between their members, producing a reduction in subgrouping in the grooming network, might have resulted from attempts to reduce tension between males.

Although subgroup structure in the arrivals networks began to match post-fission community membership patterns only in the two years preceding the fission, an association between arrival patterns and the Kasekela-Kahama division existed earlier.

Modelling revealed a significant relationship between post-split community composition and pre-split association patterns in most periods, suggesting that when the fission occurred, individuals formed communities with close pre-split associates. Similar observations have been made in a number of mammalian species, with the pattern often mediated by kinship (Holekamp et al., 1993; Metheny et al., 2008; Smouse et al., 1981; Storz, 1999; Van Horn et al., 2007). Unfortunately, without pedigree or genetic relatedness data, it is impossible to determine if kinship played a role in the community split at Gombe.

Grooming patterns were significantly associated with post-split community membership beginning only in 1971. Thus, it appears that 1971 saw an increased tendency for individuals to groom with others of the same eventual fission product, along with an increase in subgrouping in general. That the former tendency remains in 1972 while modularity decreases in the grooming network is surprising, but may reflect a balance between preferential grooming of subgroup members and efforts to groom with members of the other subgroup to reduce tension.

Ranging patterns also strongly reflected post-fission community structure in 1971 and 1972, but less so in 1970, and the fit of models using post-fission community structure to predict ranging patterns increased dramatically after 1970, again pointing to 1971 as the start of the fission.

Taken together, the concurrent and dramatic increases in modularity in the association and grooming networks and the polarization in ranging patterns support the community fission hypothesis. Additionally, subgroup membership in the association

networks only began to consistently match post-fission community structure in 1971.

The initial fluidity of subgroup membership further bolsters the conclusion that the study community underwent a transition from a single group to two coherent and increasingly distinct subgroups before fissioning.

The timing of the changes in subgrouping and ranging patterns aligned most closely with three of the four potential catalysts: the death of an older male (Leakey), a sharp increase in operational sex ratio due to a decline in reproductively cycling females, and a dominance struggle between three high-ranking males. In contrast, the last of three major changes in the feeding regimen occurred more than a year and a half earlier.

Although Leakey's death aligns with the onset of increased modularity, his low levels of betweenness centrality suggest that he was not particularly important in maintaining group cohesion. Further, limited evidence from studies of female networks supports the conclusion that animal social network structure is robust to the death of even central individuals: although female macaque networks exhibit short-term perturbations in response to the removal of high-ranking males (Flack, Girvan, de Waal, & Krakauer, 2006), in baboons the death of high-ranking males had little long-term effect on female social network properties (Franz, Altmann, & Alberts, 2015). In elephants (*Loxodonta africana*), the poaching death of older, structurally important females led to little long-term change in network structure because daughters rose to occupy their mothers' old positions (Goldenberg, Douglas-Hamilton, & Wittemyer, 2016).

As suggested by earlier authors (Bygott, 1974), more likely as a potential catalyst was the struggle for dominance between Humphrey and Charlie and Hugh. Power

struggles have been observed preceding fissions in humans (Smouse et al., 1981; Zachary, 1977) and other primates (Koyama, 1970; Nash, 1976). In particular, fissions in groups from both preindustrial and industrial societies tend to be characterized by subgroups coalescing around two leaders in conflict (Smouse et al., 1981; Zachary, 1977). Future work in chimpanzees should directly investigate the association between male hierarchy instability and changes to subgrouping patterns, and work in other species for which fissions are more common should investigate the link between hierarchy instability and group fissions.

Finally, the association between unusual sex ratio and community fission mirrors similar observations in muriquis (Tokuda et al., 2013) and macaques (Furuya, 1968). The operational sex ratio in the Kasekela group dropped after the fission, as seven adult males but only one cycling female became part of the Kahama group. However, three more females had begun to cycle by the time of the fission, which complicates the relationship between operational sex ratio and the fission. On the other hand, we did not find support for a relationship between socioeconomic sex ratio and the fission, because this ratio changed little over the study period (Figure 1c). The potential contribution of unhabituated females to the sex ratio of the Kahama community (Bygott, 1972) cannot be evaluated.

Although several authors have suggested provisioning as the primary cause of the fission and subsequent killings in Gombe (Power, 1993; Sussman, 2013), our results fail to lend support to this “anthropogenic” hypothesis. The final change in the provisioning regimen occurred more than a year and a half before the increase in modularity, and

subsequent changes to aggregation patterns at the feeding station fail to indicate that the reduction in provisioning frequency had an effect on community cohesiveness.

Similarly, fissions of a population of chacma baboons (*Papio ursinus*) were likely not mediated by food availability (Henzi, Lycett, & Piper, 1997), and both food-enhanced and wild-feeding savannah baboon (*Papio cynocephalus*) groups have been observed to fission (Van Horn et al., 2007), again suggesting that food availability alone may not be sufficient for explaining community fission in primates.

Similarly, overall group size seems to have played little role in the fission. Group size remained relatively stable between 1967 and 1972, with a maximum of 35 adults (53 total individuals). This maximum is lower than the Kasekela community size in later periods and remains well below Dunbar's (1993) predicted maximum cognitive group size of 65. It is also notable that several other communities of eastern chimpanzees have remained intact despite being much larger (Mitani et al., 2010; Nakamura, 2015).

This case study suggests that, as in other non-human primates and humans, chimpanzee community fissions may be precipitated by both hierarchy upheaval and changing sex ratios. But although group size is an important catalyst of fissions in human groups (Smouse et al., 1981), and may precipitate fissions in other primates (Henzi et al., 1997; Van Horn et al., 2007), group size is unlikely to have influenced the fission described here. This may indicate that the membership in large groups may not be as costly for chimpanzees as for other social primates, perhaps because their fission-fusion social organization means that the entire group is rarely together.

Community fissions are an important topic of study because they can shed light

on the costs and benefits of group living, and are thought to influence population genetic structure in a number of species (Storz, 1999; Whitlock & McCauley, 1990). However, fissions are rare in many species, including chimpanzees. Thus to identify the factors influencing community structure in these species, future work should investigate subgrouping, a network feature that should be more labile than group membership. Future work in chimpanzees and other species should then attempt to model the influence of male deaths, struggles for high rank, and sex ratio on community modularity using larger longitudinal data sets than presented here.

Network modularity and other forms of community detection in networks (Fortunato, 2010; Fortunato & Hric, 2016; Porter, Onnela, & Mucha, 2009) should prove a particularly fruitful avenue of study because subgrouping in social networks may influence the evolution of cooperation (Marcoux & Lusseau, 2013; Voelkl & Kasper, 2009), the development of cultural diversity (Whitehead & Lusseau, 2012), and the spread of infectious disease (Griffin & Nunn, 2012), topics of acute interest to behavioral ecologists and anthropologists.

4. Sexually Coercive Male Chimpanzees Sire More Offspring

4.1 Summary

In sexually reproducing animals, male and female reproductive strategies often conflict (Trivers, 1972). In some species, males use aggression to overcome female choice (Clutton-Brock & Parker, 1995; Smuts & Smuts, 1993), but debate persists over the extent to which this strategy is successful. Previous studies of male aggression toward females among wild chimpanzees have yielded contradictory results about the relationship between aggression and mating behavior (Muller et al., 2011, 2007, 2009a, 2009b; Pieta, 2008; Stumpf & Boesch, 2005, 2006, 2010). Critically, however, copulation frequency in primates is not always predictive of reproductive success (Curie-Cohen et al., 1983; Stern & Smith, 1984). We analyzed a 17-year sample of behavioral and genetic data from the Kasekela chimpanzee (*Pan troglodytes schweinfurthii*) community in Gombe National Park, Tanzania, to test the hypothesis that male aggression toward females increases male reproductive success. We examined the effect of male aggression toward females during ovarian cycling, including periods when the females were sexually receptive (swollen) and periods when they were not. We found that, after controlling for confounding factors, male aggression during a female's swollen periods was positively correlated with copulation frequency. However, aggression toward swollen females was not predictive of paternity. Instead, aggression by high-ranking males toward females during their nonswollen periods was positively associated with likelihood of paternity. This indicates that long-term patterns of intimidation allow high-ranking males to increase their reproductive success, supporting the sexual coercion hypothesis. To our

knowledge, this is the first study to present genetic evidence of sexual coercion as an adaptive strategy in a social mammal.

4.2 Results

The sexual coercion hypothesis predicts that male aggression against females increases male fitness (Muller et al., 2009a, 2009b; Smuts & Smuts, 1993). We tested this prediction using behavioral and genetic data from wild chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania. Female chimpanzees exhibit an anogenital swelling for about 10 days within a 36-day ovarian cycle (Goodall, 1986). During this time, a female mates with most males in the community, although high-ranking males attempt to prevent this by directing aggression toward competitors and the female herself. We consider male-female aggression during the period of maximal swelling (“swollen aggression”) as potential short-term sexual coercion (but not as forced copulation, as males rarely attempt intromission during or immediately following aggression; Muller et al., 2009a). We consider aggression occurring outside this period (“nonswollen aggression”) as potential long-term coercion. Results support the hypothesis that aggression toward a given female functions as an intimidation strategy that increases a male’s future chances of siring that female’s offspring.

4.2.1 Aggression and Paternity

We used generalized linear mixed models (GLMMs) to analyze the relationship between aggression and likelihood of paternity within dyads. We included several additional potentially influential factors (see Experimental Procedures) and used

Akaike's information criterion ($\Delta AICc$, a measure of the relative quality of a statistical model; Burnham, Anderson, & Huyvaert, 2010) to identify the best predictors of paternity. Nonswollen aggression rate, male dominance rank, the interaction between these two factors, and dyadic relatedness were important predictors of paternity (Table 7; Figure 11A). Paternity probability was greater for males of higher rank (Figure 11A and Figure 11C) but was lower if the male and female were closely related (Figure 11A and Figure 11D). Males that were more aggressive toward females during nonswollen periods were more likely to conceive with those females. Although this relationship was positive for all males, it was particularly striking among high-ranking males—a high-ranking male with the greatest rate of nonswollen aggression had a 47.9% chance of conceiving with that female (Figure 11B). Among the subset of dyads in which the male's dominance rank score was one standard deviation above the mean (standardized rank score [MDS-Z] >1, n = 47), there was a strong positive association between nonswollen aggression rate and paternity (Pearson correlation = 0.55, $p < 0.00001$; Figure 12).

Table 7: Models and effect sizes for averaged model and all models with $\Delta AICc \leq 2$.

See Methods for description of full model. *Fem Age*: centered female age (years) *Rank*: male standardized Modified David's Score (MDS-Z); *NS Agg*: standardized dyadic aggression rates towards females during their non-swollen periods; *Parity*: binary (1 = parous, 0 = nulliparous); *Despot ratio*: despotism ratio, the ratio of α -male MDS-Z to β -male MDS-Z; *Relatedness*: Queller and Goodnight's R; *S Agg*: standardized dyadic aggression rates towards females during their swollen periods. Columns with a * represent first-order interaction terms.

Effect sizes are multiplicative effects on paternity odds ratio of a one-unit change in the variable. Values above 1 will increase likelihood of paternity, while values below 1 will decrease likelihood of paternity. In Model 1, the only variable of the four significantly associated with likelihood of paternity was the interaction between male rank and non-swollen aggression ($p = 0.04$). In the averaged model, important predictors of paternity are highlighted in bold.

Model	Fem Age	Rank	NS Agg	Parity	Despot ratio	Relatedness	S Agg	NS Agg* Rank	NS Agg* Related	AICc	Δ	Weight
1		1.26	1.06			0.17		1.48		204.83	0.00	0.287
2		1.19	1.05					1.55		205.81	0.98	0.176
3		1.26	1.06	0.88		0.17		1.49		206.76	1.93	0.109
4		1.25	1.05			0.16	1.05	1.48		206.77	1.94	0.109
5	1.00	1.26	1.06			0.17		1.48		206.79	1.96	0.108
6		1.26	1.06		0.99	0.17		1.48		206.82	1.99	0.106
7		1.26	1.05			0.17		1.48	0.90	206.82	1.99	0.106
Average	1.00	1.24	1.06	0.99	1.00	0.23	1.01	1.49	0.99	-	-	-

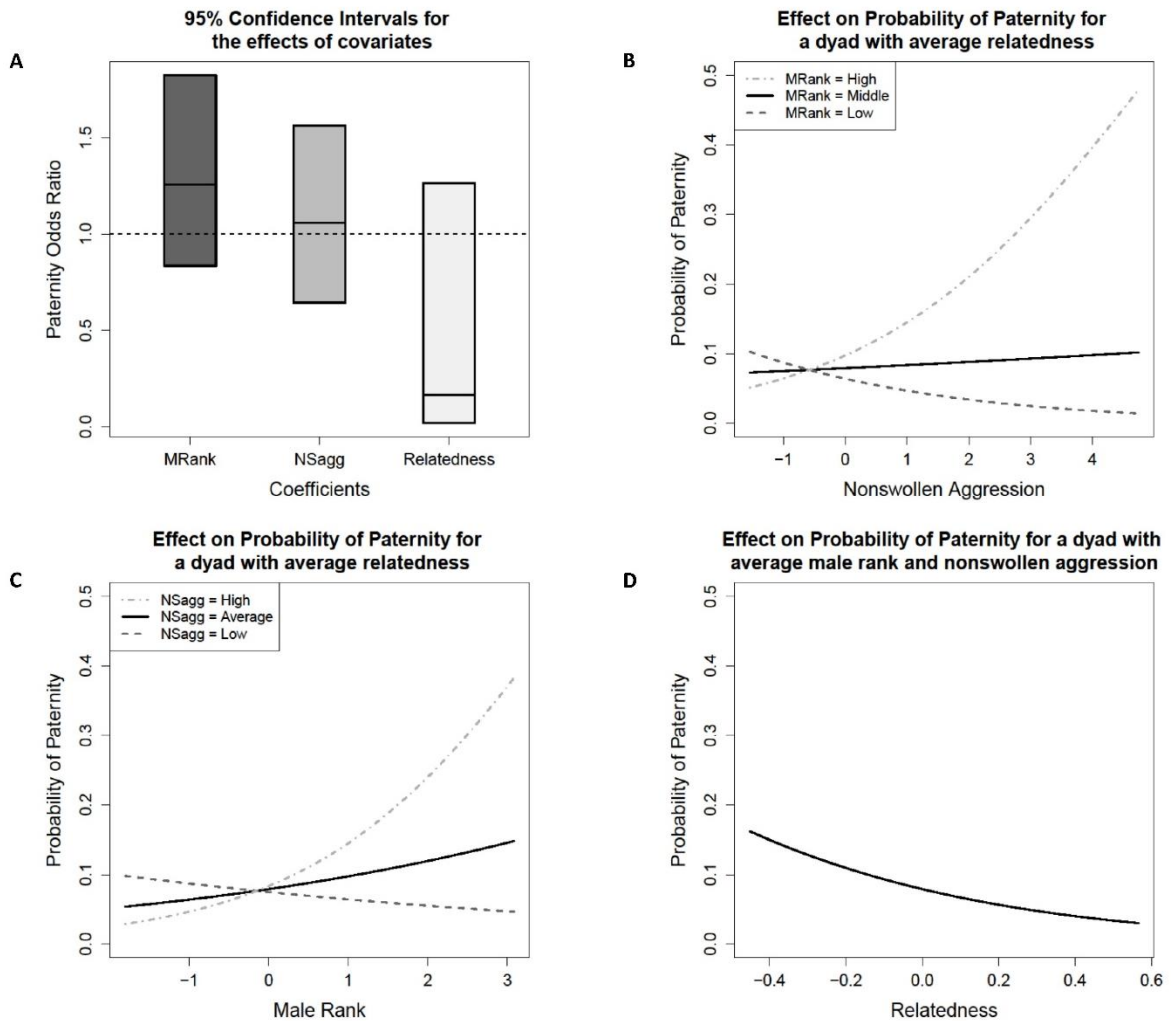


Figure 11: Predicted likelihood of paternity based on covariates from the best model.

A) Effect sizes plus 95% confidence intervals of variables from the best model (Model 1 in Table 7) on probability of paternity. MRank is standardized Modified David's Score (MDS-Z), NSagg is standardized non-swollen aggression rate, and Relatedness is Queller and Goodnight's R (see Methods).

B) Solid line indicates effect of aggression rates towards females not experiencing sexual swelling when other covariates are average; dotted line represents the effect of aggression towards non-swollen females by high-ranking males; dashed line represents effect of such aggression by low-ranking males.

C) Solid line represents the effect of MDS-Z on likelihood of paternity when other covariates are at their mean values; dotted line represents effect of male rank among dyads with males who direct high levels of aggression towards the female; dashed line represents effect of male rank among dyads with low levels of dyadic non-swollen aggression.

D) Solid line represents the effect of relatedness on likelihood of paternity among all dyads.

4.2.2 Aggression and Copulation

We used GLMMs to identify predictors of copulation rate, and again used $\Delta AICc$ as the selection criterion. We identified both swollen and nonswollen aggression rates, female age, male rank, alpha male despotism ratio (see Experimental Procedures), relatedness, and two interaction terms as the best predictors of copulation rate (Table 8). Overall, males that showed higher levels of aggression toward females tended to copulate with those females at higher rates. However, swollen aggression had the strongest association with copulation rate. Copulation rates increased with female age but were lower in closely related dyads and during periods when the alpha male was particularly dominant (high despotism ratio).

Table 8: Models and effect sizes for the average model and the best 10 models.

See Methods for description of original full model. *Fem Age*: centered female age (years) *Rank*: male standardized Modified David's Score (MDS-Z); *NS Agg*: standardized dyadic aggression rates towards females during their non-swollen periods; *Despot ratio*: despotism ratio, the ratio of α Z-MDS to β Z-MDS; *Relatedness*: Queller and Goodnight's R; *S Agg*: standardized dyadic aggression rates towards females during their swollen periods. Columns with a * represent first-order interaction terms.

Effect sizes are multiplicative effects of a one-unit change in the variable on predicted copulation rates. Values above 1 will increase predicted dyadic copulation rates, while those below 1 will decrease predicted copulation rates. In Model 1, swollen aggression rate is significantly positively correlated with copulation rate ($p < 0.000001$). Other factors significant in predicting copulations were female age ($p < 0.001$), despotism ratio ($p = 0.04$), and the interaction between swollen aggression rate and relatedness ($p = 0.03$). There was a trend towards significance for dyadic relatedness ($p = 0.07$). In the averaged model, important predictors of paternity are highlighted in bold.

Model	Fem Age	Rank	NS Agg	Despot ratio	Relatedness	S Agg	NS Agg* FemAge	NS Agg* Rank	Rank* Despot Ratio	S Agg* Relatedness	AICc	Δ	Weight
1	1.05			0.90	0.58	1.28				0.55	1610.53	0.00	0.15
2	1.05	1.23		0.90	0.55	1.28			0.95	0.54	1610.83	0.30	0.13
3	1.05	1.07		0.90	0.56	1.27				0.54	1610.85	0.32	0.13
4	1.05		1.06	0.90	0.59	1.27				0.56	1611.44	0.91	0.10
5	1.05		1.05	0.90	0.62	1.28	1.01			0.57	1611.56	1.03	0.09
6	1.05	1.07	1.06	0.90	0.57	1.26				0.55	1611.70	1.17	0.09
7	1.05	1.23	1.06	0.90	0.56	1.26			0.95	0.54	1611.71	1.18	0.08
8	1.05	1.23	1.05	0.90	0.58	1.27	1.01		0.95	0.55	1611.78	1.25	0.08
9	1.05	1.07	1.05	0.90	0.59	1.26	1.01			0.56	1611.92	1.39	0.08
10	1.05	1.22	1.06	0.90	0.59	1.26		1.06	0.95	0.51	1612.11	1.58	0.07
Average	1.05	1.10	1.03	0.90	0.58	1.27	1.00	1.00	0.98	0.55	-	-	-

4.2.3 Timing of Male-Female Aggression

To determine whether males directed more aggression at females when swollen than when nonswollen, we pooled data across the entire study period. Among dyads that spent ≥ 25 hours together during both swollen and nonswollen periods, swollen aggression rates were significantly higher than nonswollen aggression rates ($n = 549$ dyads, 2.3 [range 0 – 43.4] versus 1.5 [0 – 25.2] events per 1,000 hours together, Wilcoxon signed-rank test: $V = 32857$, $p < 0.001$). This pattern was driven by parous females; there was no difference between swollen and nonswollen aggression rates for nulliparous females ($n = 319$ dyads, 1.6 [range 0 – 22.2] versus 1.2 [0 – 25.2] events per 1,000 hours, Wilcoxon signed-rank test: $V = 6904$, $p = 0.13$).

4.2.4 Copulation and Paternity

Some primate studies have found little relationship between copulation rates and paternity (Curie-Cohen et al., 1983; Stern & Smith, 1984). However, a model including the terms from the best model for predicting paternity (nonswollen aggression, relatedness, male rank, and male rank 3 nonswollen aggression) demonstrated that copulation rate was significantly positively associated with paternity (GLMM, $z = 2.157$, $p = 0.03$).

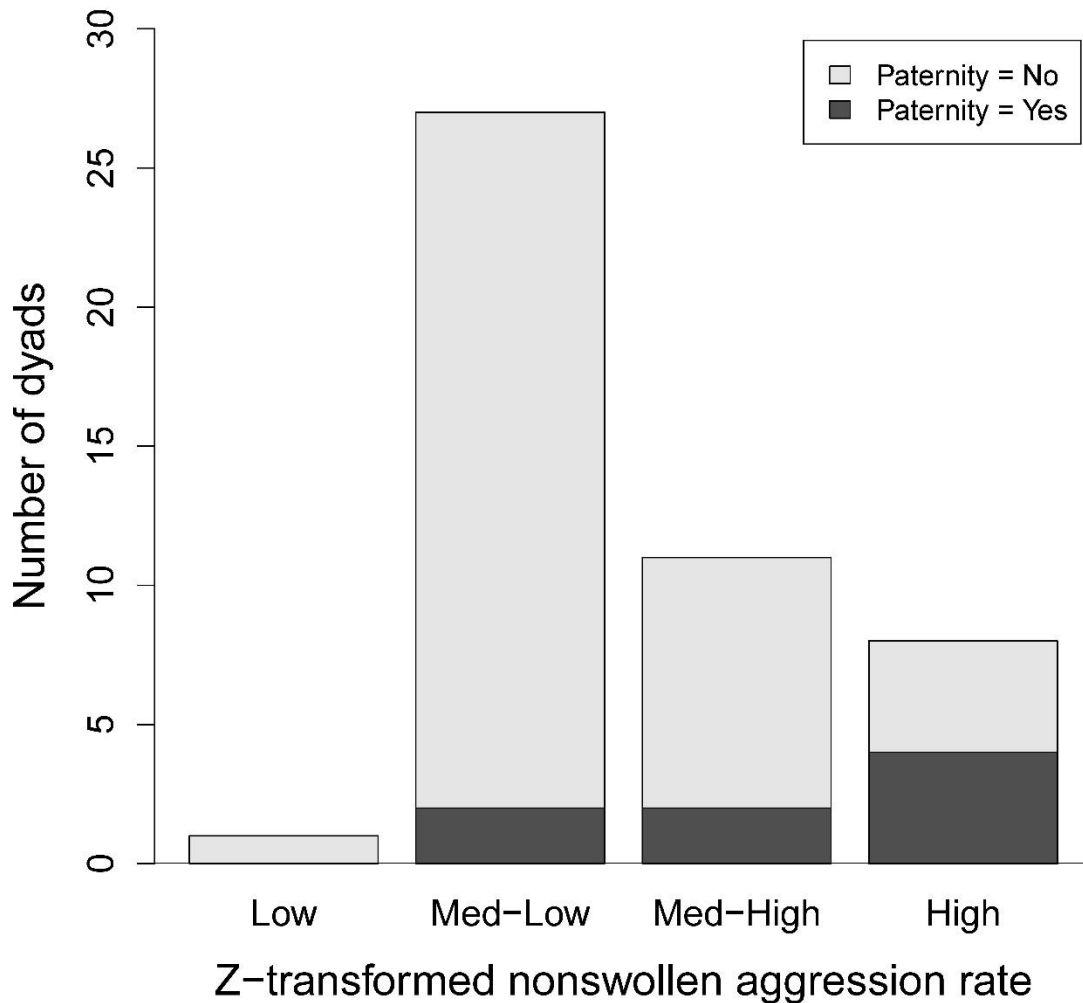


Figure 12: Paternity among highly-ranked males by non-swollen aggression rate

Observed frequency of paternities among dyads with high-ranking males ($MDS-Z > 1$) by non-swollen aggression rate. Low represents standardized aggression rates towards non-swollen females < -1 , Med-Low: $[-1, 0)$, Med-High: $[0, 1)$, and High: ≥ 1 .

4.3 Discussion

In this study of wild chimpanzees, aggression toward non-swollen females was positively associated with paternity, particularly among high-ranking males. This

indicates that at Gombe, sexual coercion (as long-term intimidation) is a strategy that high-ranking males successfully employ to increase fitness. Male rank was also positively associated with paternity, independently of aggression. Although this could indicate female preference for dominant males, the relationship between aggression and paternity in high-ranking males indicates that patterns of paternity did not arise from unfettered female choice. Instead, the rank effect is most likely a consequence of mate guarding by dominant males (Muller et al., 2009a; Muller & Wrangham, 2004a). Copulation data also support the sexual coercion hypothesis. Males that directed high levels of aggression toward swollen females, and to a lesser extent nonswollen females, exhibited higher copulation rates. However, although copulation rate predicted paternity, males who were particularly aggressive toward swollen females were not more likely to sire those females' offspring. This is probably because swollen females experience temporal variation in fertility, with fertilization most likely during the periovulatory period (POP) (Deschner, Heistermann, Hodges, & Boesch, 2003; Emery Thompson, 2005). Therefore, aggression toward swollen females may allow some (e.g., low-ranking) males to increase their mating success, but only during nonfertile portions of the females' swollen periods. This may also explain the finding that although males directed more aggression toward swollen females, only aggression toward nonswollen females increased paternity likelihood, especially for high-ranking males. Also, as the dominance of the alpha increased relative to other males, overall copulation rates decreased. This is intriguing evidence for effective mate guarding by strong alpha males and is consistent with previous work suggesting that alpha males sometimes trade mating access to females for

coalitionary support (Duffy et al., 2007). “Despotic” alphas may need less support and thus may retain a greater share of copulations. As with paternity, male rank was positively correlated with copulation rate, probably due to mate guarding by high-ranking males.

This is the first genetic test of the sexual coercion hypothesis in any mammal. Importantly, our molecular and behavioral data accord extremely well with extensive behavioral evidence of long-term (indirect) sexual coercion in the Kanyawara chimpanzee (*P. t. schweinfurthii*) community in Kibale National Park, Uganda, where dyadic copulation rate and male aggression were also positively correlated (Muller et al., 2007). As in our study, males displayed increased aggression toward parous females when they were sexually receptive. Additionally, copulations during the POP were correlated with aggression throughout the ovarian cycle (Muller et al., 2011), demonstrating the importance of long-term coercion at Kanyawara (Muller et al., 2009a). Higher-ranking males were the most frequent aggressors toward females (Muller et al., 2009a), and when the alpha was present, there were fewer female solicitations (of other males) (Muller et al., 2011), demonstrating the alpha’s effectiveness at mate guarding. Our finding that older females copulated more often than younger females is consistent with data from Kanyawara showing that older females are more attractive to males (Muller, Thompson, & Wrangham, 2006) and that parous females are more often the target of male aggression (Wrangham, 2002). Such strong accord between two research sites provides confidence in the robustness of these findings, certainly among eastern chimpanzees.

By contrast, research on western chimpanzees (*P. t. verus*) in Tai National Park, Côte d'Ivoire, found no evidence for sexual coercion, suggesting instead that females successfully employ mate choice (Stumpf & Boesch, 2005, 2006, 2010). There are several possible explanations for these contrasting results. At Tai, where females are more gregarious than at Gombe and Kanyawara (Wittiger & Boesch, 2013), there may be fewer opportunities to “sneak” copulations in a more cohesive group, and thus less incentive for high-ranking males to use aggression to attempt to constrain female choice. Furthermore, our study community had similar numbers of adult males to Kanyawara (11–14 and 10–11 adult males, respectively) (Muller et al., 2011, 2007) but more than double the number of adult males found in the two Tai communities studied (3–4 adult males) (Stumpf & Boesch, 2010). In smaller groups, reproductive success tends to correlate more closely with rank than in larger groups (Alberts, 2003; Cowlshaw & Dunbar, 1991; Wrangham, 2002). Thus, a high-ranking male in a small group may not need to resort to coercion to obtain a large share of paternities.

More comparative work is needed to disentangle the effects of biological and demographic differences on the prevalence and efficacy of male sexual coercion. Although the results from Gombe and Kanyawara clearly demonstrate that sexual coercion can be an effective component of sexual selection in chimpanzees, it remains to be seen whether coercion is a ubiquitous phenomenon, and whether alternative strategies exist. Further work is also needed to determine the mechanism by which long-term patterns of aggression increase paternity probability. Understanding the context in which nonswollen aggression by high-ranking males occurs and how those males interact with

female recipients of coercion during swollen periods may shed light on why this strategy is effective for only some individuals.

4.4 Experimental Procedures

We used data from the long-term study of the Kasekela community at Gombe National Park. We analyzed data from a 17-year period (1995–2011) for which relatedness and paternity information was available from analysis of DNA obtained from fecal samples (Gilby, Brent, et al., 2013; Wroblewski et al., 2009). During daily, all-day focal follows of adult chimpanzees, researchers continuously recorded group composition, reproductive state of all females, and all observed aggressive and copulation events in the focal chimpanzee's party (Goodall, 1986; Wilson, 2012). We restricted analyses to “reproductive windows,” i.e., when a given female was experiencing ovarian cycles. For nulliparous females, this period started at sexual maturity and ended with their first conception. For parous females, this was the interval between the first sexual swelling after postpartum amenorrhea and the next conception. We estimated conception dates by backdating 226 days from the offspring's date of birth (Boehm & Pusey, 2013).

For analysis of copulation rates and paternity odds, we used data from reproductive windows during which offspring of known paternity were conceived, and from those dyads observed together during both swollen (mean \pm SD = 275 \pm 271 hour) and nonswollen periods (312 \pm 283 hour). The difference between these two means is not statistically significant ($t = 21.7568$, $p = 0.079$). Adult males were at least 12 years of age, the age of the youngest known sire at Gombe (Gilby, Brent, et al., 2013; Wroblewski et al., 2009). We classified females as adult after their first copulation with an adult male

(for natal females) or immigration date. The data set contained 31 reproductive windows (among 21 adult females) and 18 adult males, forming 250 unique dyads and 338 dyad-reproductive windows.

We defined aggressive events as directed displays, chases, or contact aggression by one or more males toward a single female. We calculated rates of aggression for each dyad (aggression events per 1,000 hours together) and then standardized them by Z-transformation within each reproductive window. Thus, dyadic aggression rates represented a male's aggression rate relative to a female's average rate of received aggression from all males during a particular reproductive window. We classified aggression according to whether it occurred during the swollen period of a female's ovarian cycle (swollen aggression) or the nonswollen period (nonswollen aggression). Male rank was calculated for each window using the modified David's score (MDS) method (de Vries et al., 2006b), using submissive pant-grunt data from the year leading up to the end of the window. Because the maximum possible MDS in any period is proportional to the square of the number of individuals being ranked, we standardized the MDS scores by Z-transformation (MDS-Z) within each reproductive window to facilitate comparison between periods. We calculated a "despotism ratio" for each period to quantify the magnitude of rank difference between the alpha and beta male by dividing the MDS of the highest-ranking male by that of the second-highest. Finally, females were considered parous after having had one pregnancy carried to term and nulliparous otherwise.

To determine whether male aggression toward females increased in reproductive

contexts, we pooled party association and aggression data for each dyad across the entire 17-year study period. Subjects for this analysis were 38 cycling adult females and 20 adult males forming 549 dyads that spent at least 25 hours together during both swollen and nonswollen periods.

Of the 31 infants included in the study, paternities for 19 were previously reported by Wroblewski et al. (2009) and for four by Gilby et al. (2013). Eight new paternities were identified for this study using DNA extracted from fecal samples. Fecal samples were collected and preserved in an equal volume of RNAlater (Ambion), and DNA was extracted using the QIAamp DNA Stool Mini Kit (QIAGEN) as described in Wroblewski et al. (2009). Individual genotypes were determined for 8–11 microsatellite loci through PCR amplification and allele sizing. Candidate males for paternity of each offspring were those that were R9 years of age at the time of conception. The offspring, mother, and candidate male genotypes were compared across all loci, and in every case, only one male (the father) could have contributed the complementary set of alleles to the offspring, given the maternal genotype. All other males had mismatches with the offspring and maternal genotypes at R1 locus. Relatedness between males and females was calculated using Kinship v1.3.1 (Goodnight & Queller, 1999) and is the same as the frequency-based calculations established by Queller and Goodnight (1989).

4.4.1 Analyses

For the GLMMs, we used swollen and nonswollen aggression rates to represent short- and long-term coercion efforts by males, respectively. We included in our full models the following factors, which, in addition to aggression, might influence paternity

and copulation rates. Female age is known to influence male chimpanzee mating interest (Muller et al., 2006). Male rank could increase dyadic paternity odds and copulation rates for dominant males via mate guarding (Muller & Wrangham, 2004a; Watts, 1998) or female preferences (Matsumoto-Oda, 1999). We included parity (nulliparous or parous) as a factor to determine whether it mediates the effect of male aggression on reproductive success as predicted by the “cost of sexual attractiveness” hypothesis (Wrangham, 2002). As alpha males may trade mating access for coalitionary support (Duffy et al., 2007), a more despotic alpha may receive a higher share of paternities because he needs less support. Therefore, we calculated the despotism ratio (alpha MDS-Z/beta MDS-Z) for each reproductive window. Finally, we included dyadic relatedness because evidence from birds and mammals (Crnokrak & Roff, 1999; Pusey, 1980; Ralls, Ballou, & Templeton, 1988) suggests a cost to inbreeding, and Gombe chimpanzees are known to actively avoid mating with close relatives (Pusey, 1980, 2005). We included all first-order interactions between both swollen and non-swollen aggression and these main effects, with the exception of despotism ratio. This we only included in a first-order interaction with male rank, as despotism ratio would seem unlikely to mediate the efficacy of male aggression.

All analyses were performed in R (R Development Core Team, 2014) using the lme4 package (Bates et al., 2014) for all GLMMs, and the MuMIn package for model selection (Bartoń, 2015). For all models, we determined the best set of predictors using AIC as the model selection criterion (Anderson, Burnham, & Thompson, 2000; Burnham et al., 2010) and ranked the resulting models by ΔAIC_c , considering those with values ≤ 2

(with respect to the best model) to have substantial support (Burnham & Anderson, 1998). We then used model averaging (Burnham & Anderson, 1998) to generate final parameter estimates based on this set of plausible models.

2.4.1.1 Paternity

To test whether aggression was correlated with likelihood of paternity, we ran a series of GLMM regressions, with paternity (yes/no) as the dependent variable, our candidate predictors of paternity and first-order interactions as factors, and female ID as a random effect. By standardizing aggression rates, we accounted for most of the variability that could be attributed to individual males. We therefore did not include male ID as a random effect in our final models, although inclusion resulted in minimal or no change in our parameter estimates.

2.4.1.2 Copulation Rate

To test whether aggression was correlated with copulation rates, we ran negative binomial GLMM regressions for count data (data overdispersion prevented the use of Poisson regression), with copulation counts as the outcome variable, time spent together as an offset, female ID as a random effect, and our candidate predictors of copulation rate (and first-order interaction terms) as factors. We did not account for zero inflation because the zero-inflated model produced no increase of fit over the standard model.

2.4.1.3 Copulation Rate versus Likelihood of Paternity

To test whether copulation rates were positively correlated with likelihood of paternity, we ran a logistic GLMM regression, with paternity (yes/no) as the outcome variable, female ID as a random effect, and the four terms from the best model for

predicting paternity, plus copulation rate, as factors.

5. Conclusions and future directions

The studies presented here reveal clues to the adaptive value of male sociality and the mechanisms by which cooperation influences fitness in male chimpanzees. They also reveal the relationship between male social behavior and community cohesion, and the forces that cause communities to divide. Finally, they reveal the efficacy of male aggression for constraining female choice in eastern chimpanzees. These projects point towards future comparative work to assess the generalizability of results to communities of different sizes, taxa, and demographics. They also point towards detailed studies of mechanism and chronology to understand the proximate effects of male sociality and coercive aggression on fitness and social structure.

5.1 Future work emerging from Chapter 2

The results presented in Chapter 2 require further analysis to determine the causal relationship between grooming, rank change, and reproductive success. The association between grooming others and rank change and reproductive success may result from low-ranking males grooming high-ranking males in exchange for tolerance and support, as has been suggested in other species (Hemelrijk, 1994; Seyfarth, 1977; Seyfarth & Cheney, 1984). This hypothesis predicts that males that successfully rise in rank or sire offspring would preferentially groom high-ranking males (particularly if they were low-ranking), while unsuccessful males would groom others indiscriminately. Alternatively, the results presented in Chapter 2 may result from successful males grooming others as consolation for failing to mate with estrous females. This would predict that males that

achieve mating success would concentrate their grooming particularly on unsuccessful males. In turn, successful males would *be* groomed by all other males indiscriminately. On the other hand, unsuccessful males would groom others indiscriminately, while being groomed particularly by successful males.

Further, because rates of received grooming were negatively associated with siring success but positively associated with rank change, perhaps high-ranking males might be excluding males rising in rank, which predicts a positive association between rank increase and receipt of aggression from other males in mating contexts. I will use long-term grooming data to test these hypotheses and predictions. Traditionally, analysis of cooperative exchange has relied on correlated rates of cooperative behavior over extended periods (Hemelrijk, 1990a, 1990b), but a more targeted analysis of grooming patterns is required to interpret the results from Chapter 2.

Complementing this proposed project, and the work presented in Chapter 2, are my three seasons of field research in Gombe National Park studying the mechanisms by which cooperative exchange, or alternatively particular social bonds, might function to increase individual fitness. To do this, I collected grooming, proximity, and association data, as well as urine samples for hormone extraction, to determine whether grooming with a high-ranking male is exchanged for support or tolerance, and whether this behavior lowers stress hormone levels. I will also identify preferred social partners (those individuals sharing social bonds) from patterns of affiliative behavior, and, taking advantage of the fluctuating composition of chimpanzee foraging parties, determine whether the presence of a preferred social partner is associated with lower rates of

received aggression, higher rates of aggression towards others, and lower levels of stress hormones. Thus, my field work addresses the proximate value of bonds and cooperative exchange, while analysis of long-term data presented in Chapter 2 addresses the ultimate value of these behaviors.

Recently, researchers have begun to recognize limitations of the traditional approach to analyzing animal social interactions by dyad; in particular, this approach fails to account for the non-independence of those interactions. For example two individuals could associate frequently because of a strong social bond, or because they both have strong bonds with a third individual. Network analysis allows for the explicit accounting for such non-independence when modelling animal social behavior. The relationship between grooming, social bonds, and coalitionary support remains uncertain in chimpanzees and other primates, and this problem lends itself well to the use of statistical models of social networks, wherein ties between individuals are treated as random variables. In particular, exponential random graph models (ERGMs, or p^* models), are well-suited to single observations of large networks, and Siena (or stochastic actor oriented models, or SOAMs) model transitions (e.g. the dissolution or formation of a social bond) and therefore are well-suited for longitudinal datasets such our own (Block, Stadtfeld, & Snijders, 2016; Robins, Pattison, Kalish, & Lusher, 2007; Snijders, 2011; Snijders, Bunt, & Steglich, 2010; Wasserman & Faust, 1994).

In addition to dyadic cooperation, I am interested in investigating group decision making in chimpanzees. One promising avenue of study is threshold models of collective action, according to which the costs and benefits of alternative decisions (such as

“participate in or abstain from a riot”) depend on the number or fraction of other actors who have chosen each alternative (Granovetter, 1978). Variation in individual cost/benefit “thresholds” to action determine both individual decisions and group behavior (Granovetter, 1978). These models describe human behavior in a number of contexts, including riots, political revolutions, and abrupt shifts in public opinion (Granovetter, 1978; Kuran, 1995). Threshold models also accord well with group behavior in chimpanzee hunts (Gilby, 2006; Gilby et al., 2015; Gilby, Eberly, & Wrangham, 2008), and may also apply to territorial patrolling behavior (Gilby, Wilson, & Pusey, 2013). The success of these models in chimpanzees and humans suggests potential wider application in studies of chimpanzee group decision making.

Such models may be appropriate when the cost of engaging in the activity in question is high, such as hunting or patrolling, but other, more democratic processes may determine group decision-making when individuals choose among less costly options, such as group movement. In the latter scenario, key individuals could still play an outsized role in determining group movement if they were more knowledgeable about the terrain, such as in hamadryas baboons (*Papio hamadryas*: Kummer, 1968, 2013), or if they were higher ranking, such as in Barbary macaques (*Macaca sylvanus*: Seltsmann et al., 2016). Alternatively, group movement could be determined by simple rules of thumb, such as in olive baboons (*Papio anubis*) (Amornbunchornvej et al., 2016; Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015). Studies of group decision making will investigate the interface between leadership, dominance, and cooperation.

5.2 Future work emerging from Chapter 3

Follow-up studies are also needed to further explore the results presented in Chapter 3 showing that a male dominance struggle and a change in operational sex ratio were the most likely catalysts of the Gombe community fission. Because these results were based on a single fission event, they should be viewed as hypotheses about the factors that influence community structure in chimpanzees. This realization has prompted a comparative project investigating the predictors of community structure in two communities of east African chimpanzees, in Gombe and in Kibale National Park, Uganda. In this project, I am investigating the factors associated with subgrouping (which changes much more frequently than group membership) to gain insight into the factors that systematically influence community cohesion, and thereby the costs of group living. This project utilizes 35 years of data on male networks from the long-term Gombe database, along with a comparative 10-year sample from the Ngogo community in Kibale. Preliminary results suggest that, of the factors identified as potential fission catalysts, only dominance hierarchy upheavals are systematically associated with increased subgrouping. In addition, evidence suggests that the number of males, both in a within-group analysis and between groups, is strongly positively associated with subgrouping, as is season.

In future work I will extend these efforts to probe the relative costs and benefits of group living in relation to social network structure, with the intention of making broader comparisons between and among non-human primate and human groups. For example, I have identified several social and ecological factors that influence social structure in

males. But because socioecological models predict different constraints on male and female sociality, further work is needed comparing male and female network structure. These socioecological models can be tested more generally by extending my analytical framework to female networks, and to data from other species. In turn, I hope to investigate how social structure might influence individual fitness.

5.3 Future work emerging from Chapter 4

Results presented in Chapter 4 lend themselves to several interpretations; the differing evidence of sexual coercion from studies in Tai, Gombe, and Kanyawara suggest that the efficacy of sexual coercion might vary between communities of different size or different subspecies. A subsequent comparative study in two communities of eastern chimpanzees found further that the efficacy of male sexual coercion can depend on the nature of the male dominance hierarchy. In the despotic Sonso community in Budongo Forest, Uganda, male aggression was the best predictor of copulation rates within male-female dyads, while in the more egalitarian Mahale M-group male grooming of females, rather than male aggression, was positively associated with copulation rates (Kaburu & Newton-Fisher, 2015b). However, as these authors neglected to account for the influence of male rank in their analyses of coercion, further work is needed to determine which factors (group size, subspecies, or despotism) moderate male reproductive tactics. Thus I am pursuing two follow-up projects that investigate diversity and strategic plasticity of male reproductive behavior.

The first project investigates the role of demography in moderating the efficacy of different sexually-selected reproductive tactics. In primate groups, as the number of

males increases, high rank alone often becomes insufficient for monopolizing access to females, so males may resort to other tactics to increase their reproductive success (Alberts, 2003; Alberts et al., 2006; Boesch et al., 2006; Cowlshaw & Dunbar, 1991). Thus conflicting evidence of sexual coercion might result from differences in community sizes in different field sites. Alternatively, conflicting results could arise because of subspecies or ecological differences at different field sites. I will test these competing hypotheses by contrasting the efficacy of male coercion in the Kasekela community (our initial study community) with that in the smaller neighboring Mitumba community, thereby avoiding the confounding effects of subspecies and ecological differences. Further, an expanded dataset will afford more statistical power to investigate the effect of hierarchy despotism on the efficacy of different male reproductive tactics.

Second, I will investigate the efficacy of alternative male reproductive tactics beyond sexual coercion. Using a dataset updated with newly extracted data from long-term field notes, I test whether affiliative behavior towards females also increases males' reproductive success, accounting for aggression and other factors associated with male reproductive success (Feldblum et al., 2014; Chapter 4). Data extraction is ongoing, but preliminary results suggest that, controlling for coercive aggression, grooming may also play a role in male reproductive success. Yet grooming and coercion do not represent alternative male reproductive strategies, because there is no relationship between male-female grooming and aggression. Instead, these likely represent distinct tactics (*sensu* Davies, Krebs, & West, 2012) individual males employ, sometimes in concert, to increase their reproductive success.

5.4 Forward

My research overall aspires to investigate the interplay between competition and cooperation within and between groups, how such forces among individuals influence social structure, and how social structure in turn affects the lives of individuals. Future work will integrate additional network-based and hormonal methods, and expand to include females and comparisons between field sites and species, to contribute novel insights into the evolution of primate sociality.

Appendix A: Supplementary figures and tables

See next page

Table 9: Best models predicting rank change using frequency-based measures of grooming effort and CSI.

The list of models within 2 AICc points of the best model for predicting rank change (full data set; no coalitions). “age: prime” and “age: old” represent the effects of being a *prime* and *old* male, respectively, relative to being a *young* male. “betw CSI” represents the effect of betweenness in the network of dyadic CSIs, “CSI” is the summed CSI measure, “Elo beg” is the measure of Z-transformed Elo score at the start of a period, “Grm IN time” and “Grm OUT time” are cumulative time grooming others and being groomed, and “Elo beg: Grm IN time” and “Elo beg: Grm OUT time” are the interactions between Elo score at the start of a period and grooming times.

Model	intercept	age: prime	age: old	betw CSI	CSI	Tot obs.	Elo beg	Grm IN time	Grm OUT time	Elo beg: Grm IN time	Elo beg: Grm OUT time	Δ AICc	Akaike weight
1	26.37					60.88	-130.59	76.23				0.00	0.15
2	34.66					64.22	-126.19	70.67	11.28		-29.87	0.73	0.11
3	40.73			-227.32		62.70	-129.78	66.47				0.80	0.10
4	34.04					66.43	-126.45	77.50		-16.48		1.06	0.09
5	25.26					54.30	-130.07	69.13	15.22	43.31	-68.58	1.29	0.08
6	-9.07				5.50	62.53	-131.07	59.29	3.41		-35.06	1.47	0.07
7	-22.67				6.82	64.42	-125.75		47.13		-34.42	1.56	0.07
8	-0.83				3.27	59.55	-133.65	64.88				1.67	0.07
9	75.86	+	+			56.85	-112.75	93.72	-4.16		-36.07	1.88	0.06
10	31.20					66.80	-118.41		68.05		-26.98	1.94	0.06
avg (best mods)	18.53	-3.59	-4.86	-41.82	2.05	61.44	-127.85	56.93	12.39	5.39	-25.22		
se (best)	41.99	17.17	22.92	120.80	3.89	18.91	21.59	41.48	31.63	22.50	30.66		
avg (all mods)	26.10	-12.02	-15.72	-104.53	2.19	59.59	-126.32	54.80	11.81	5.28	-22.73		
se (all)	46.99	29.99	38.59	175.49	3.95	21.17	22.21	43.27	33.55	25.83	32.98		

Table 10: Best models for predicting rank change using rate-based measures and including betweenness in the network of coalition formation

Column names are the same as in Table 9, except the CSI and grooming measures are constructed with rates of component behaviors and “Coalit. Between” is the betweenness in the network of coalition formation.

model	intercept	age: prime	age: old	betw CSI	CSI	Coalit. Between	Elo beg	Grm IN rate	Grm OUT rate	Elo beg: Grm IN rate	Elo beg: Grm OUT rate	ΔAICc	Akaike weight
1	82.88	+	+			52.32	-70.94	45.12	-15.23	47.86	-72.83	0.00	0.15
2	108.15	+	+			51.18	-52.47	37.78				0.27	0.13
3	-160.33				37.10	54.02	-83.34	-0.25	-32.36	67.56	-96.33	0.62	0.11
4	93.75	+	+			52.72	-35.00					0.66	0.11
5	15.19					55.82	-79.71	21.67	-7.11	65.43	-92.27	1.14	0.08
6	111.23	+	+			46.79	-64.14	55.13	-22.05		-30.71	1.20	0.08
7	98.15	+	+	-180.47		51.32	-67.13	41.41	-19.60	51.85	-79.09	1.30	0.08
8	15.33	+	+		17.12	50.28	-44.55					1.47	0.07
9	-34.66	+	+		23.13	51.22	-74.92	29.02	-29.48	51.76	-77.80	1.58	0.07
10	97.43	+	+			46.27	-44.15		8.05		-30.07	1.84	0.06
11	111.26	+	+			46.31						1.92	0.06
avg (best mods)	48.06	-77.87	-96.79	-14.09	6.88	51.24	-58.61	23.25	-11.31	27.71	-45.10		
se (best)	104.34	55.20	67.14	67.78	16.69	18.40	29.99	33.84	24.55	34.09	44.45		
avg (all mods)	50.79	-80.98	-98.04	-36.58	7.55	47.21	-52.50	20.13	-10.43	15.98	-30.62		
se (all)	108.00	58.71	70.17	110.44	17.97	21.69	31.02	32.74	24.82	30.10	40.53		

Table 11: Best models for predicting reproductive success, coalitions dataset

List of best models and model-averaged parameter estimates, using the coalitions dataset. Column names match previous tables.

Model	Age: prime	Age: old	CSI	Total sired	Coalit. Between	Grm IN rate	Grm OUT rate	MDS	MDS: Grm IN rate	MDS: Grm OUT rate	Δ AICc	Akaike weight
1				1.40		0.23	2.96	1.87		0.57	0.00	0.10
2				1.43		0.19	3.63	1.73	1.65	0.39	0.34	0.08
3			1.77	1.44		0.12	2.70	1.57	1.84	0.34	0.48	0.08
4			1.68	1.40		0.16	2.24	1.70		0.53	0.58	0.07
5						0.24	2.83	1.87		0.63	0.73	0.07
6			2.03	1.31		0.26					0.95	0.06
7						0.25	2.42	1.81			1.02	0.06
8			2.00			0.28					1.06	0.06
9				1.31		0.25	2.42	1.79			1.10	0.06
10	+	+				0.27	3.41	2.12		0.58	1.11	0.06
11			1.64			0.17	2.13	1.73		0.60	1.35	0.05
12	+	+		1.34		0.28	3.42	2.03		0.53	1.45	0.05
13						0.20	3.39	1.75	1.54	0.45	1.47	0.05
14			2.01			0.23		1.45			1.57	0.04
15			1.74			0.13	2.52	1.61	1.71	0.40	1.63	0.04
16			2.02	1.30		0.23		1.42			1.74	0.04
17			1.54			0.19	1.85	1.70			1.94	0.04
avg (best mods)	0.89	1.00	1.34	1.19		0.21	2.24	1.64	1.14	0.63		
avg (all mods)	0.78	1.00	1.29	1.16	1.06	0.25	2.02	1.52	1.11	0.71		

Table 12: Betweenness in the male affiliative networks

Values are normalized betweenness centrality scores in the joint arrivals networks in each period. We standardized the betweenness scores by z-transformation within each period and added a color scale for ease of interpretation.

males	1967 b	1968 a	1968 b	1969 a	1969 b	1970 a	1970 b	1971 a	1971 b	1972 a	1972 b
CH	-0.88	-0.57	-0.83	-0.15	-0.54	-0.51	0.55	-0.59	-0.48	-0.71	
DE	1.73	3.35	1.78	0.7	2.8	3.43	-0.46	2.81	-0.48	-0.71	0.57
EV	1.66	0.1	1.93	0.75	-0.54	-0.51	-0.64	-0.66	0.05	0.49	0.92
FB	0.79	0.91	-0.12	0.81	-0.31	0.36	0.77	-0.07	-0.42	-0.2	-0.68
FG	0.99	-0.57	-0.61	-0.11	-0.54	-0.4	-0.66	-0.52	-0.89	-0.44	-0.68
GI	-0.76	0.14	-0.89	1.61	-0.54	-0.51	-0.67	-0.71	-0.74	-0.27	
GOL	-0.39	-0.49	0.59	1.08	-0.26	-0.03	-0.47	-0.44	-0.52	0.07	0.39
HG	-0.88	-0.56	-0.89	-0.97	-0.54	-0.51	-0.17	-0.71	-0.55	1.83	1.22
HH	1.94	-0.42	-0.89	-0.87	-0.54	-0.15	-0.43	-0.68	0.2	0.94	-0.68
HM	-0.55	-0.57	1.87	-0.97	-0.54	-0.51	-0.67	0.81	-0.05	-0.79	-0.68
JJ			-0.83	-0.93	-0.15	-0.22	0.68	-0.07	-0.09	2.4	2.35
LK	-0.85	0.28	-0.89	-0.65	-0.35	-0.39	-0.25				
MK	-0.33	-0.57	-0.89	-0.97	-0.54	-0.37	-0.63	0.48	2.9	-0.59	-0.68
PP	-0.18	-0.17	-0.08								
RX	-0.79	-0.57	-0.11								
SF									1.31	-0.79	-0.68
ST	-0.73	-0.57	0.1	1.95	1.22	-0.18	-0.08	-0.67	-0.89	-0.79	-0.68
WW	-0.32	0.89	0.1	-0.65	1.4	0.52	3.13	1.03	0.67	-0.43	-0.68
WZ	-0.45	-0.57	0.67	-0.66							

References

- Adams, E. S. (1990). Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in colony size. *Animal Behaviour*, *39*(2), 321–328. [https://doi.org/10.1016/S0003-3472\(05\)80877-2](https://doi.org/10.1016/S0003-3472(05)80877-2)
- Alberts, S. C. (1995). Balancing Costs and Opportunities: Dispersal in Male Baboons. *The American Naturalist*, *145*(2), 279–306.
- Alberts, S. C. (2003). Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal Behaviour*, *65*(4), 821–840. <https://doi.org/10.1006/anbe.2003.2106>
- Alberts, S. C., Buchan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: from mating opportunities to paternity success. *Animal Behaviour*, *72*(5), 1177–1196. <https://doi.org/10.1016/j.anbehav.2006.05.001>
- Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual Review of Ecology and Systematics*, *5*, 325–383.
- Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., ... Pulliam, J. R. C. (2003). Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 517–547. <https://doi.org/10.1146/annurev.ecolsys.34.030102.151725>
- Altmann, S. A. (1962). A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Sciences*, *102*.
- Amornbunchornvej, C., Brugere, I., Strandburg-Peshkin, A., Farine, D., Crofoot, M. C., & Berger-Wolf, T. Y. (2016). FLICA : A Framework for Leader Identification in Coordinated Activity. *arXiv*.
- Anderson, D. R., Burnham, K. P., & Thompson, W. L. (2000). Null Hypothesis Testing: Problems, Prevalence, and an Alternative. *Journal of Wildlife Management*, *64*(4), 912–923.
- Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences*, *218*.
- Arnold, K., & Whiten, A. (2003). Grooming Interactions Among the Chimpanzees of the

- Budongo Forest, Uganda: Tests of Five Explanatory Models. *Behaviour*, 140, 519–552.
- Aureli, F., & Schaffner, C. M. (2002). Relationship assessment through emotional mediation. *Behaviour*, 139(2), 393–420.
- Aureli, F., & Whiten, A. (2003). Emotions and behavioral flexibility. In D. Maestriepieri (Ed.), *Primate Psychology* (pp. 289–323). Cambridge: Harvard University Press.
- Barrett, L., & Henzi, S. P. (2002). Constraints on Relationship Formation among Female Primates. *Behaviour*, 139(2), 263–289.
- Barrett, L., Henzi, S. P., & Rendall, D. (2007). Social brains, simple minds: does social complexity really require cognitive complexity? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 362(1480), 561–75. <https://doi.org/10.1098/rstb.2006.1995>
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 266(1420), 665–670. <https://doi.org/10.1098/rspb.1999.0687>
- Bartoń, K. (2015). MuMIn: Multi-model inference. Retrieved from <http://cran.r-project.org/package=MuMIn>
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., & Dai, B. (2014). lme4 package.
- Berghänel, A., Ostner, J., Schröder, U., & Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, 81(6), 1109–1116. <https://doi.org/10.1016/j.anbehav.2011.02.009>
- Block, P., Stadtfeld, C., & Snijders, T. A. B. (2016). Forms of Dependence: Comparing SAOMs and ERGMs From Basic Principles. *Sociological Methods & Research*, 1–38. <https://doi.org/10.1177/0049124116672680>
- Boehm, E. E., & Pusey, A. E. (2013). Measuring gestation length in the chimpanzees of Gombe National Park. *American Journal of Physical Anthropology*, 150 Suppl, 64–301. <https://doi.org/10.1002/ajpa.22247>
- Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai Forest: Behavioural ecology and evolution*. Oxford University Press.
- Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Tai forest. *American Journal of Physical Anthropology*, 130(1), 103–15. <https://doi.org/10.1002/ajpa.20341>

- Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). *Ucinet for Windows: Software for Social Network Analysis*. Harvard, MA: Analytic Technologies.
- Bray, J., Pusey, A. E., & Gilby, I. C. (2016). Incomplete control and concessions explain mating skew in male chimpanzees. *Proceedings of the Royal Society B-Biological Sciences*, in press. <https://doi.org/10.1098/rspb.2016.2071>
- Brent, L. J. N. (2015). Friends of friends: Are indirect connections in social networks important to animal behaviour? *Animal Behaviour*, *103*, 211–222. <https://doi.org/10.1016/j.anbehav.2015.01.020>
- Brent, L. J. N., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A. G., ... Platt, M. L. (2013). Genetic origins of social networks in rhesus macaques. *Scientific Reports*, *3*(January), 1042. <https://doi.org/10.1038/srep01042>
- Burnham, K. P., & Anderson, D. R. (1998). *Model selection and inference: a practical information-theoretic approach*. New York: Springer Verlag New York.
- Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2010). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23–35. <https://doi.org/10.1007/s00265-010-1029-6>
- Burt, R. S. (2009). *Structural holes: The social structure of competition*. Harvard University Press.
- Bygott, J. D. (1972). Cannibalism among Wild Chimpanzees. *Nature*, *238*, 410–411.
- Bygott, J. D. (1974). *Agonistic behaviour and dominance in wild chimpanzees*. University of Cambridge.
- Bygott, J. D. (1979). Agonistic behaviour and dominance among wild chimpanzees of the Gombe National Park. In D. A. Hamburg & E. R. McCown (Eds.), *The Great Apes* (pp. 405–428). Menlo Park: Benjamin/ Cummings.
- Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(33), 13850–3. <https://doi.org/10.1073/pnas.0900639106>
- Carlson, A. (1986). Group Territoriality in the Rattling Cisticola, *Cisticola chiniana*. *Oikos*, *47*(2), 181–189.
- Chagnon, N. A. (1975). Genealogy, solidarity, and relatedness: Limits to local group size

- and patterns of fissioning in an expanding population. *Yearbook of Physical Anthropology*, 19, 95–110.
- Chapais, B. (1995). Alliances as a Means of Competition in Primates: Evolutionary, Developmental, and Cognitive Aspects. *Yearbook of Physical Anthropology*, 38, 115–136.
- Chapman, C. a., Chapman, L. J., & Wrangham, R. W. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, 36(1), 59–70. <https://doi.org/10.1007/BF00175729>
- Chepko-Sade, B. D., & Olivier, T. J. (1979). Coefficient of Genetic Relationship and the Probability of Intragenealogical Fission in *Macaca mulatta*. *Behavioral Ecology and Sociobiology*, 5, 263–278.
- Chepko-Sade, B. D., & Sade, D. S. (1979). Patterns of group splitting within matrilineal kinship groups - A study of social group structure in *Macaca mulatta* (Cercopithecidae: Primates). *Behavioral Ecology and Sociobiology*, 5(1), 67–86. <https://doi.org/10.1007/BF00302696>
- Cheverud, J. M., Buettner-Janusch, J., & Sade, D. S. (1978). Social Group Fission and the Origin of Intergroup Genetic Differentiation among the Rhesus Monkeys of Cayo Santiago. *American Journal of Physical Anthropology*, 49, 449–456.
- Clauset, A., Newman, M. E. J., & Moore, C. (2004). Finding community structure in very large networks. *Physical Review E*, 70(6), 66111. <https://doi.org/10.1103/PhysRevE.70.066111>
- Clutton-Brock, T. H. (1998). Reproductive skew, concessions and limited control. *TREE*, 13(7), 288–292.
- Clutton-Brock, T. H., & Parker, G. A. (1992). Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology*, 67(4), 437–456.
- Clutton-Brock, T. H., & Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour*, 49(5), 1345–1365. <https://doi.org/10.1006/anbe.1995.0166>
- Cohen, S., Gottlieb, B. H., & Underwood, L. G. (2000). Social Relationships and Health. In S. Cohen, L. G. Underwood, & B. H. Gottlieb (Eds.), *Social Support Measurement and Intervention* (pp. 3–25). New York: Oxford University Press.
- Collins, D. A., Sindimwo, A., & Goodall, J. (2006). Serial group divisions in the olive baboons of Gombe National Park, Tanzania. In *XXIst Congress of the International Primatological Society*. Entebbe, Uganda.

- Connor, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin “super-alliance.” *Proceedings of the Royal Society B*, 268, 263–267. <https://doi.org/10.1098/rspb.2000.1357>
- Constable, J. L., Ashley, M. V, Goodall, J., & Pusey, A. E. (2001). Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology*, 10(5), 1279–300. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/11380884>
- Cowlishaw, G., & Dunbar, R. I. M. (1991). Dominance rank and mating success in male primates. *Animal Behaviour*, 41, 1045–1056.
- Crnokrak, P., & Roff, D. a. (1999). Inbreeding depression in the wild. *Heredity*, 83 (Pt 3)(January 1998), 260–70. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10504423>
- Crockford, C., Wittig, R. M., Langergraber, K. E., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 280(January).
- Csárdi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Systems*, 1695, 1695.
- Curie-Cohen, M., Yoshihara, D., Luttrell, L., Benafordo, K., MacCluer, J. W., & Stone, W. H. (1983). The effects of dominance on mating behavior and paternity in a captive troop of rhesus monkeys (*Macaca mulatta*). . *American Journal of Primatology*, 5, 127–138.
- Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. John Murray. Retrieved from <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:The+descent+of+man#3>
- Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An Introduction to Behavioural Ecology* (4th Editio). Wiley-Blackwell.
- de Villiers, M. S., Richardson, P. R. K., & van Jaarsveld, A. S. (2003). Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*). *Journal of Zoology*, 260, 377–389. <https://doi.org/10.1017/S0952836903003832>
- de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006a). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, 71(3), 585–592. <https://doi.org/10.1016/j.anbehav.2005.05.015>

- de Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006b). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, *71*(3), 585–592. <https://doi.org/10.1016/j.anbehav.2005.05.015>
- de Waal, F. B. M. (1982). *Chimpanzee Politics*. Baltimore: The John's Hopkins University Press.
- de Waal, F. B. M. (2000). Primates — A Natural Heritage of Conflict Resolution. *Science*, *289*(July), 586–591.
- Dekker, D., Krackhardt, D., & Snijders, T. A. B. (2007). Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika*, *72*(4), 563–581.
- Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes* verus. *Animal Behaviour*, *66*(3), 551–560. <https://doi.org/10.1006/anbe.2003.2210>
- Dittus, W. P. J. (1988). Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Animal Behaviour*, *36*(6), 1626–1645. [https://doi.org/10.1016/S0003-3472\(88\)80104-0](https://doi.org/10.1016/S0003-3472(88)80104-0)
- Drews, C. (1993). The Concept and Definition of Dominance in Animal Behavior. *Behavior*, *125*(3–4), 283–313. <https://doi.org/10.1017/CBO9781107415324.004>
- Duffy, K. G., Wrangham, R. W., & Silk, J. B. (2007). Male chimpanzees exchange political support for mating opportunities. *Current Biology*, *17*(15), 586–587.
- Dugatkin, L. A. (1997). *Cooperation among animals : an evolutionary perspective*. New York: Oxford University Press.
- Dunbar, R. I. M. (1988). *Primate Social Systems*. London: Croom Helm.
- Dunbar, R. I. M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, *31*(1), 35–49. <https://doi.org/10.1007/BF00167814>
- Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, *16*, 681–735.
- Eberle, M., & Kappeler, P. M. (2004). Sex in the dark: determinants and consequences of mixed male mating tactics in *Microcebus murinus*, a small solitary nocturnal primate. *Behavioral Ecology and Sociobiology*, *57*(1), 77–90. <https://doi.org/10.1007/s00265-004-0826-1>

- Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B, Biological Sciences*, (January), 489–505. <https://doi.org/10.1098/rstb.2006.1991>
- Emery Thompson, M. (2005). Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): methodological considerations and the role of hormones in sex and conception. *American Journal of Primatology*, 67(1), 137–58. <https://doi.org/10.1002/ajp.20174>
- ESRI. (2010). ArcGIS desktop. Redlands, CA: Environmental Systems Research Institute.
- Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, 425(October), 785–791.
- 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. <https://doi.org/10.1016/j.cub.2014.10.039>
- Fix, A. G. (1975). Fission-fusion and lineal effect: aspects of the population structure of the Semai Senoi of Malaysia. *American Journal of Physical Anthropology*, 43(2), 295–302. <https://doi.org/10.1002/ajpa.1330430216>
- Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, 439(7075), 426–429. <https://doi.org/10.1038/nature04326>
- 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*, 6, 1–11. <https://doi.org/10.1038/srep35404>
- Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey, A. E. (2015). Social bonds in the dispersing sex: partner preferences among adult female chimpanzees. *Animal Behaviour*, 105, 139–152. <https://doi.org/10.1016/j.anbehav.2015.04.012>
- Fortunato, S. (2010). Community detection in graphs. *Physics Reports*, 486(3–5), 75–174. <https://doi.org/10.1016/j.physrep.2009.11.002>
- Fortunato, S., & Hric, D. (2016). Community detection in networks: A user guide. *Physics Reports*, 659, 1–44. <https://doi.org/10.1016/j.physrep.2016.09.002>
- Fox, J., & Monette, G. (1992). Generalized collinearity diagnostics. *Journal of the*

American Statistical Association, 87(417).

- Franz, M., Altmann, J., & Alberts, S. C. (2015). Knockouts of high-ranking males have limited impact on baboon social networks. *Current Zoology*, 61(1), 107–113.
- Freeman, L. C. (1979). Centrality in Social Networks Conceptual Clarification. *Social Networks*, 1(3), 215–239. [https://doi.org/10.1016/0378-8733\(78\)90021-7](https://doi.org/10.1016/0378-8733(78)90021-7)
- Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences of the United States of America*, 107(46), 19949–54. <https://doi.org/10.1073/pnas.1007997107>
- Friesen, T. M. (1999). Resource structure, scalar stress, and the development of Inuit social organization. *World Archaeology*, 31(1), 21–37. <https://doi.org/10.1080/00438243.1999.9980430>
- Furuya, Y. (1968). On the fission of troops of Japanese monkeys. *Primates*, 10(1), 47–69. <https://doi.org/10.1007/BF01730809>
- Galdikas, B. M. F. (1985). Subadult male orangutan sociality and reproductive behavior at Tanjung Puting. *American Journal of Primatology*, 8(2), 87–99. <https://doi.org/10.1002/ajp.1350080202>
- Gandon, S. (1999). Kin Competition, the Cost of Inbreeding and the Evolution of Dispersal. *Journal of Theoretical Biology*, 200(4), 345–364. <https://doi.org/10.1006/jtbi.1999.0994>
- Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour*, 71(4), 953–963. <https://doi.org/10.1016/j.anbehav.2005.09.009>
- Gilby, I. C. (2012). Cooperation among Non-kin: Reciprocity, Markets, and Mutualism. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *Evolution of Primate Societies* (pp. 514–530). Chicago: University of Chicago Press.
- Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, 67(3), 373–381. <https://doi.org/10.1007/s00265-012-1457-6>
- Gilby, I. C., Eberly, L. E., & Wrangham, R. W. (2008). Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation. *Animal Behaviour*, 75(2), 351–360. <https://doi.org/10.1016/j.anbehav.2007.06.008>

- Gilby, I. C., Machanda, Z. P., Mjungu, D. C., Rosen, J., Muller, M. N., Pusey, A. E., & Wrangham, R. W. (2015). "Impact hunters" catalyze cooperative hunting in two wild chimpanzee communities. *Philosophical Transactions of the Royal Society, Series B, Biological Sciences*, 370, 20150005. <https://doi.org/http://dx.doi.org/10.1098/rstb.2015.0005>
- Gilby, I. C., Wilson, M. L., & Pusey, A. E. (2013). Ecology rather than psychology explains co-occurrence of predation and border patrols in male chimpanzees. *Animal Behaviour*, 86(1), 61–74. <https://doi.org/10.1016/j.anbehav.2013.04.012>
- Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, 62(11), 1831–1842. <https://doi.org/10.1007/s00265-008-0612-6>
- Gillespie, T. R., & Chapman, C. A. (2001). Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. *Behavioral Ecology and Sociobiology*, 50, 329–338. <https://doi.org/10.1007/s002650100371>
- Goldberg, T. L., & Wrangham, R. W. (1997). Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA. *Animal Behaviour*, 54, 559–570.
- Goldenberg, S. Z., Douglas-Hamilton, I., & Wittemyer, G. (2016). Vertical Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks. *Current Biology*, 26(1), 75–79. <https://doi.org/10.1016/j.cub.2015.11.005>
- Gomes, C. M., & Boesch, C. (2011). Reciprocity and trades in wild West African chimpanzees. *Behavioral Ecology and Sociobiology*, 65(11), 2183–2196. <https://doi.org/10.1007/s00265-011-1227-x>
- Gompper, M. E., Gittleman, J. L., & Wayne, R. K. (1997). Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. *Animal Behaviour*, 53(4), 781–797. <https://doi.org/10.1006/anbe.1996.0344>
- Good, B. H., De Montjoye, Y. A., & Clauset, A. (2010). Performance of modularity maximization in practical contexts. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, 81(4), 1–19. <https://doi.org/10.1103/PhysRevE.81.046106>
- Goodall, J. (1965). Chimpanzees of the Gombe Stream Reserve. In I. Devore (Ed.), *Primate Behavior: Field Studies of Monkeys and Apes* (pp. 425–473). New York: Holt, Rinehart and Winston.
- Goodall, J. (1983). Population dynamics during a 15 year period in one community of

- freeliving chimpanzees in the Gombe National Park, Tanzania. *Zeitschrift Fuer Tierpsychologie*, 61(1), 1–60.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Belknap Press of Harvard University Press.
- Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., ... Riss, D. (1979). Intercommunity Interactions in the Chimpanzee Population of the Gombe National Park. In D. A. Hamburg & E. R. McCown (Eds.), *The Great Apes* (pp. 12–53). San Francisco: Benjamin/ Cummings.
- Goodnight, K. F., & Queller, D. C. (1999). Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Molecular Ecology*, 8, 1231–1234.
- Granovetter, M. (1978). Threshold Models of Collective Behavior. *American Journal of Sociology*, 83(6), 1420–1443.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28(4), 1140–1162. [https://doi.org/10.1016/S0003-3472\(80\)80103-5](https://doi.org/10.1016/S0003-3472(80)80103-5)
- Griffin, R. H., & Nunn, C. L. (2012). Community structure and the spread of infectious disease in primate social networks. *Evolutionary Ecology*, 26(4), 779–800. <https://doi.org/10.1007/s10682-011-9526-2>
- Grinnell, J., Packer, C., & Pusey, A. E. (1995). Cooperation in male lions: kinship, reciprocity or mutualism? *Animal Behaviour*, 49(1), 95–105. [https://doi.org/10.1016/0003-3472\(95\)80157-X](https://doi.org/10.1016/0003-3472(95)80157-X)
- Hammerstein, P. (2003). Why is reciprocity so rare in social animals? A protestant appeal. In P. Hammerstein (Ed.), *Genetic and cultural evolution of cooperation* (pp. 83–93). Cambridge, MA: MIT Press.
- Hammerstein, P., & Noe, R. (2016). Biological trade and markets. *Philosophical Transactions of the Royal Society B, Biological Sciences*, 371, 20150101. <https://doi.org/10.1098/rstb.2015.0101>
- Hemelrijk, C. K. (1990a). A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. *Journal of Theoretical Biology*, 143, 405–420. [https://doi.org/10.1016/S0003-3472\(05\)80775-4](https://doi.org/10.1016/S0003-3472(05)80775-4)
- Hemelrijk, C. K. (1990b). Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behavior*, 39, 1013–1029.

- Hemelrijk, C. K. (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, *48*, 479–481. Retrieved from <http://www.sciencedirect.com.sire.ub.edu/science/article/pii/S0003347284712644#>
- Hemelrijk, C. K., & Ek, A. (1991). Reciprocity and interchange of grooming and “support” in captive chimpanzees. *Animal Behaviour*, *41*(6), 923–935. [https://doi.org/10.1016/S0003-3472\(05\)80630-X](https://doi.org/10.1016/S0003-3472(05)80630-X)
- Henzi, S. P., & Barrett, L. (2002). Infants as a commodity in a baboon market. *Animal Behaviour*, *63*(5), 915–921. <https://doi.org/10.1006/anbe.2001.1986>
- Henzi, S. P., & Barrett, L. (2007). Coexistence in Female-Bonded Primate Groups. *Advances in the Study of Behavior*, *37*(7), 43–81. [https://doi.org/10.1016/S0065-3454\(07\)37002-2](https://doi.org/10.1016/S0065-3454(07)37002-2)
- Henzi, S. P., Lycett, J. E., & Piper, S. E. (1997). Fission and troop size in a mountain baboon population. *Animal Behaviour*, *53*(3), 525–535. <https://doi.org/10.1006/anbe.1996.0302>
- Hill, K. R., Barton, M., & Hurtado, A. M. (2009). The Emergence of Human Uniqueness: Characters Underlying Behavioral Modernity. *Evolutionary Anthropology*, *20*, 187–200. <https://doi.org/10.1002/evan.20224>
- Hill, K. R., Walker, R. S., Bozicević, M., Eder, J., Headland, T., Hewlett, B., ... Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science (New York, N.Y.)*, *331*(6022), 1286–1289. <https://doi.org/10.1126/science.1199071>
- Holekamp, K. E., Ogutu, J. O., Dublin, H. T., & Smale, L. (1993). Fission of a Spotted Hyena Clan: Consequences of Prolonged Female Absenteeism and Causes of Female Emigration. *Ethology*, *93*, 285–299.
- Holt-Lunstad, J., Smith, T. B., & Layton, J. B. (2010). Social relationships and mortality risk: a meta-analytic review. *PLoS Medicine*, *7*(7), e1000316. <https://doi.org/10.1371/journal.pmed.1000316>
- House, J. S., Landis, K. R., & Umberson, D. (1988). Social Relationships and Health. *Science (New York, N.Y.)*, *241*(4865), 540–5. <https://doi.org/10.1126/science.3399889>
- Hunley, K. L., Spence, J. E., & Merriwether, D. A. (2008). Macaque Societies: A Model for the Study of Social Organization. *American Journal of Physical Anthropology*, *135*, 195–205. <https://doi.org/10.1002/ajpa>
- Hurd, J. (1983). Church Fissioning and Kin Relatedness among the “Nebraska” Amish of

- Pennsylvania. *Social Biology*, 30(1), 59–66.
<https://doi.org/10.1080/19485565.1983.9988516>
- Inoue, E., Inoue-Murayama, M., Vigilant, L., Takenaka, O., & Nishida, T. (2008). Relatedness in wild chimpanzees: influence of paternity, male philopatry, and demographic factors. *American Journal of Physical Anthropology*, 137(3), 256–262. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/18512686>
- Jack, K. M., & Fedigan, L. (2004). Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 1: Patterns and causes of natal emigration. *Animal Behaviour*, 67(4), 761–769. <https://doi.org/10.1016/j.anbehav.2003.04.015>
- Janson, C. H., & van Schaik, C. P. (1988). Recognizing the Many Faces of Primate Food Competition: Methods. *Behaviour*, 105(1), 165–186.
- Johnson, G. A. (1982). Organizational Structure and Scalar Stress. In C. Renfrew, M. J. Rowlands, & B. A. Segraves (Eds.), *Theory and Explanation in Archaeology* (pp. 389–422). New York: Academic Press.
- Kaburu, S. S. K., Inoue, S., & Newton-Fisher, N. E. (2013). Death of the Alpha: Within-Community Lethal Violence Among Chimpanzees of the Mahale Mountains National Park. *American Journal of Primatology*, 75(8), 789–797. <https://doi.org/10.1002/ajp.22135>
- Kaburu, S. S. K., & Newton-Fisher, N. E. (2015a). Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 99, 61–71. <https://doi.org/10.1016/j.anbehav.2014.10.018>
- Kaburu, S. S. K., & Newton-Fisher, N. E. (2015b). Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. *Behavioral Ecology and Sociobiology*, 69(6), 1039–1052. <https://doi.org/10.1007/s00265-015-1917-x>
- Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., & Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology*, 73(8), 758–767. <https://doi.org/10.1002/ajp.20914>
- Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford, California: Stanford University Press.
- Kappeler, P. M., & van Schaik, C. P. (2004). Sexual selection in primates: review and selective preview. In P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual Selection in Primates: New and Comparative Perspectives* (pp. 3–23). Cambridge: Cambridge

University Press.

- Kapsalis, E. (2003). Matrilineal kinship and primate behavior. In B. Chapais & C. M. Berman (Eds.), *Kinship and Behavior in Primates* (pp. 153–176). Oxford University Press.
- Koyama, N. (1970). Changes in Dominance Rank and Division of a Wild Japanese Monkey Troop in Arashiyama. *Primates*, *11*, 335–390.
<https://doi.org/10.1007/BF01731037>
- Krackhardt, D. (1988). Predicting with networks: nonparametric multiple regression analysis of dyadic data. *Social Networks*, *10*, 359–381.
- Krause, J., & Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press.
- Kuester, J., & Paul, A. (1997). Group Fission in Barbary Macaques (*Macaca sylvanus*) at Affenberg Salem. *International Journal of Primatology*, *18*(6), 941–966.
- Kummer, H. (1968). *Social Organization of Hamadryas Baboons*. Chicago, London: The University of Chicago Press.
- Kummer, H. (1971). *Primate Societies: Group Techniques of Ecological Adaptation*. (W. Goldschmidt, Ed.). Chicago: Aldine Atherton.
- Kummer, H. (1978). On the value of social relationships to nonhuman primates: A heuristic scheme. *Social Science Information*, *17*(4–5), 687–705.
<https://doi.org/10.1177/053901847801700418>
- Kummer, H. (2013). Sources of Productive Questions: Experiences of a Primatologist. *Nova Acta Leopoldina*, *111*(380), 157–167.
- Kuran, T. (1995). *Private Truths, Public Lies: The Social Consequences of Preference Falsification*. Cambridge, Massachusetts: Harvard University Press.
- Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *PNAS*, *104*(19), 7786–7790.
- Lehmann, J., & Boesch, C. (2008). Sexual Differences in Chimpanzee Sociality. *International Journal of Primatology*, *29*(1), 65–81. <https://doi.org/10.1007/s10764-007-9230-9>
- Lukas, D., Reynolds, V., Boesch, C., & Vigilant, L. (2005). To what extent does living in a group mean living with kin? *Molecular Ecology*, *14*(7), 2181–2196.
<https://doi.org/10.1111/j.1365-294X.2005.02560.x>

- Mange, A. P. (1964). Growth and inbreeding of a human isolate. *Human Biology*, 36(2), 104–133.
- Manno, T. G., Dobson, F. S., Hoogland, J. L., & Foltz, D. W. (2007). Social Group Fission and Gene Dynamics Among Black-Tailed Prairie Dogs (*Cynomys Ludovicianus*). *Journal of Mammalogy*, 88(2), 448–456. <https://doi.org/10.1644/06-MAMM-A-099R1.1>
- Manson, J. H., & Wrangham, R. W. (1991). Intergroup Aggression in Chimpanzees and Humans. *Current Anthropology*, 32(4).
- Marcoux, M., & Lusseau, D. (2013). Network modularity promotes cooperation. *Journal of Theoretical Biology*, 324, 103–108. <https://doi.org/10.1016/j.jtbi.2012.12.012>
- Markham, A. C., Alberts, S. C., & Altmann, J. (2012). Intergroup conflict: ecological predictors of winning and consequences of defeat in a wild primate population. *Animal Behaviour*, 84(2), 399–403. <https://doi.org/10.1016/j.anbehav.2012.05.009>
- Matsumoto-Oda, A. (1999). Female choice in the opportunistic mating of wild chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. *Behavioral Ecology and Sociobiology*, 46(4), 258–266.
- McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences of the United States of America*, 104(26), 10910–4. <https://doi.org/10.1073/pnas.0701159104>
- McElreath, R., Clutton-Brock, T. H., Fehr, E., Fessler, D. M. T., Hagen, E. H., Hammerstein, P., ... Wilson, M. I. (2003). Group Report: The role of cognition and emotion in cooperation. In P. Hammerstein (Ed.), *Genetic and cultural evolution of cooperation* (pp. 125–152). Cambridge, MA: MIT Press.
- McKenna, J. J. (1978). Biosocial Functions of Grooming Behavior among the Common Indian Langur Monkey (*Presbytis entellus*). *American Journal of Physical Anthropology*, 48, 503–509.
- Ménard, N., & Vallet, D. (1993). Dynamics of fission in a wild Barbary macaque group (*Macaca sylvanus*). *International Journal of Primatology*, 14(3), 479–500. <https://doi.org/10.1007/BF02192778>
- Metheny, J. D., Kalcounis-Rueppell, M. C., Bondo, K. J., & Brigham, R. M. (2008). A genetic analysis of group movement in an isolated population of tree-roosting bats. *Proceedings of the Royal Society B: Biological Sciences*, 275(1648), 2265–2272. <https://doi.org/10.1098/rspb.2008.0532>
- Miller, J. A., Pusey, A. E., Gilby, I. C., Schroepfer-Walker, K., Markham, A. C., &

- Murray, C. M. (2013). Competing for space: female chimpanzees are more aggressive inside than outside their core areas. *Animal Behaviour*, *87*, 147–152. <https://doi.org/10.1016/j.anbehav.2013.10.023>
- Missakian, E. A. (1973). The Timing of Fission among Free-ranging Rhesus Monkeys. *American Journal of Physical Anthropology*, *38*, 621–624.
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. <https://doi.org/10.1016/j.anbehav.2008.11.021>
- Mitani, J. C., & Amstler, S. J. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869–884.
- Mitani, J. C., Gros-Louis, J., & Richards, A. F. (1996). Sexual Dimorphism, the Operational Sex Ratio, and the Intensity of Male Competition in Polygynous Primates. *The American Naturalist*, *147*(6), 113–146.
- Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, *59*(4), 885–893. <https://doi.org/10.1006/anbe.1999.1389>
- Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, *61*(5), 915–924. <https://doi.org/10.1006/anbe.2000.1681>
- Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, *70*(5), 1079–1086. <https://doi.org/10.1016/j.anbehav.2005.02.012>
- Mitani, J. C., Watts, D. P., & Amstler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology : CB*, *20*(12), R507-8. <https://doi.org/10.1016/j.cub.2010.04.021>
- Mitani, J. C., Watts, D. P., Pepper, J. W., & Merriwether, D. A. (2002). Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour*, *64*, 727–737. <https://doi.org/10.1006/anbe.2002.4014>
- Mjungu, D. C., Wilson, M. L., Foerster, S., & Pusey, A. E. (2015). Fighting back: Population recovery and expansion of the range size of the Mitumba chimpanzee community in Gombe National Park, Tanzania. In *International Primatological Society Meeting*. Chicago.
- Moffett, M. W. (2013). Human identity and the evolution of societies. *Human Nature (Hawthorne, N.Y.)*, *24*(3), 219–67. <https://doi.org/10.1007/s12110-013-9170-3>
- Møller, A. P. (1988). Ejaculate quality, testes size and sperm competition in primates.

Journal of Human Evolution, 17(5), 479–488. [https://doi.org/10.1016/0047-2484\(88\)90037-1](https://doi.org/10.1016/0047-2484(88)90037-1)

- Møller, A. P., Dufva, R., & Allander, K. (1993). Parasites and the evolution of host social behavior. In *Advances in the Study of Behavior*, Vol. 22 (pp. 65–102). Academic Press. Inc.
- Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, 78(2), 359–370. <https://doi.org/10.1016/j.anbehav.2009.04.024>
- Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos* (pp. 112–124). Cambridge: Cambridge University Press.
- Muller, M. N., Emery Thompson, M., Kahlenberg, S. M., & Wrangham, R. W. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology*, 65(5), 921–933. <https://doi.org/10.1007/s00265-010-1093-y>
- Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings. Biological Sciences / The Royal Society*, 274(1612), 1009–14. <https://doi.org/10.1098/rspb.2006.0206>
- Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2009a). Male aggression against females and sexual coercion in chimpanzees. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females* (pp. 184–217). Cambridge: Harvard University Press.
- Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2009b). Male Aggression and Sexual Coercion of Females in Primates. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual Coercion in Primates and Humans* (pp. 3–22). Cambridge, MA: Harvard Univ Press.
- Muller, M. N., & Mitani, J. C. (2005). Conflict and Cooperation in Wild Chimpanzees. *Advances in the Study of Behavior*, 35, 275–331. [https://doi.org/10.1016/S0065-3454\(05\)35007-8](https://doi.org/10.1016/S0065-3454(05)35007-8)
- Muller, M. N., Thompson, M. E., & Wrangham, R. W. (2006). Male chimpanzees prefer mating with old females. *Current Biology : CB*, 16(22), 2234–2238. <https://doi.org/10.1016/j.cub.2006.09.042>
- Muller, M. N., & Wrangham, R. W. (2004a). Dominance, aggression and testosterone in

- wild chimpanzees: a test of the “challenge hypothesis.” *Animal Behaviour*, 67(1), 113–123. <https://doi.org/10.1016/j.anbehav.2003.03.013>
- Muller, M. N., & Wrangham, R. W. (2004b). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 55(4), 332–340. <https://doi.org/10.1007/s00265-003-0713-1>
- Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology*, 17, 1020–1028. <https://doi.org/10.1093/beheco/arl042>
- Nakamura, M. (2015). Demography of the M group. In M. Nakamura, K. Hosaka, N. Itoh, & K. Zamma (Eds.), *Mahale Chimpanzees: 50 Years of Research* (pp. 82–93). Cambridge: Cambridge University Press.
- Nash, L. T. (1976). Troop fission in free-ranging baboons in the Gombe Stream National Park, Tanzania. *American Journal of Physical Anthropology*, 44(1), 63–77. <https://doi.org/10.1002/ajpa.1330440109>
- Neel, J. V. (1967). The genetic structure of primitive human populations. *Japanese Journal of Human Genetics*, 12(1), 16.
- Neel, J. V., & Salzano, F. M. (1967). Further studies on the Xavante Indians: Some hypotheses-generalizations resulting from these studies. *American Journal of Human Genetics*, 19(4), 554–74. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/1706315> <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1706315&tool=pmcentrez&rendertype=abstract>
- Newman, M. E. J. (2006a). Finding community structure in networks using the eigenvectors of matrices. *Physical Review E*, 74(3), 36104. <https://doi.org/10.1103/PhysRevE.74.036104>
- Newman, M. E. J. (2006b). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences*, 103(23), 8577–82. <https://doi.org/10.1073/pnas.0601602103>
- Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E*, 69, 1–15. <https://doi.org/10.1103/PhysRevE.69.026113>
- Newton-Fisher, N. E. (2004). Hierarchy and social status in Budongo chimpanzees. *Primates*, 45(2), 81–87. <https://doi.org/10.1007/s10329-003-0064-6>
- Newton-Fisher, N. E., Emery Thompson, M., 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), 417–28. <https://doi.org/10.1002/ajpa.21241>
- Nishida, T. (1968). The Social Group of Wild Chimpanzees in the Mahali Mountains. *Primates*, 9, 167–224.
- Nishida, T. (1983). Alpha Status and Agonistic Alliance in Wild Chimpanzees (*Pan troglodytes schweinfurthii*). *Primates*, 24(3), 318–336.
- Nishida, T., & Kawanaka, K. (1972). Inter-unit group relations among wild chimpanzees in the Mahali mountains. *Kyoto University African Studies*, 7, 131–169.
- Noë, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, 35(1), 1–11.
- Okamoto, K., & Matsumura, S. (2001). Group Fission in Moor Macaques (*Macaca maurus*). *International Journal of Primatology*, 22(3), 481–493.
- Olsen, C. L. (1987). The demography of colony fission from 1878–1970 among the Hutterites of North America. *American Anthropologist*, 89(7), 823–837. <https://doi.org/10.1525/aa.1987.89.4.02a00040>
- Ostner, J., & Schülke, O. (2014). The evolution of social bonds in primate males. *Behaviour*, 151, 1–36. <https://doi.org/10.1163/1568539X-00003191>
- Patzelt, A., Kopp, G. H., Ndao, I., Kalbitzer, U., Zinner, D., & Fischer, J. (2014). Male tolerance and male-male bonds in a multilevel primate society. *Proceedings of the National Academy of Sciences of the United States of America*. <https://doi.org/10.1073/pnas.1405811111>
- 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. <https://doi.org/10.1023/A:1020760616641>
- Perrin, N., & Mazalov, V. (1999). Dispersal and Inbreeding Avoidance. *The American Naturalist*, 154(3), 282–292. <https://doi.org/10.1086/303236>
- Perrin, N., & Mazalov, V. (2000). Local Competition, Inbreeding, and the Evolution of Sex-Biased Dispersal. *The American Naturalist*, 155(1), 116–127. <https://doi.org/10.1086/303296>
- Pieta, K. (2008). Female Mate Preferences Among *Pan troglodytes schweinfurthii* of Kanyawara, Kibale National Park, Uganda. *International Journal of Primatology*, 29(4), 845–864. <https://doi.org/10.1007/s10764-008-9282-5>

- Pitcher, T. J., Magurran, A. E., & Winfield, I. J. (1982). Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology*, *10*(2), 149–151. <https://doi.org/10.1007/BF00300175>
- Porter, M. a., Onnela, J.-P., & Mucha, P. J. (2009). Communities in Networks. *American Mathematical Society*, *56*(9), 0–26. <https://doi.org/10.1016/j.physrep.2009.11.002>
- Power, M. (1993). *The Egalitarians - Human and Chimpanzee*. Cambridge: Cambridge University Press.
- Pusey, A. E. (1979). Intercommunity transfer of chimpanzees in Gombe National Park. In D. A. Hamburg & E. R. McCown (Eds.), *The Great Apes* (pp. 465–480). Menlo Park: Benjamin/ Cummings.
- Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour*, *28*, 543–552.
- Pusey, A. E. (2005). Inbreeding Avoidance in Primates. In A. P. Wolf & W. H. Durham (Eds.), *Inbreeding, Incest, and the Incest Taboo* (pp. 61–75). Stanford: Stanford University Press.
- Pusey, A. E., & Packer, C. (1987a). Dispersal and Philopatry. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 251–266). University of Chicago Press.
- Pusey, A. E., & Packer, C. (1987b). The evolution of sex-biased dispersal in lions. *Behaviour*, *101*(4), 275–310.
- 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. <https://doi.org/10.1098/rstb.2013.0077>
- Queller, D. C., & Goodnight, K. F. (1989). Estimating Relatedness Using Genetic Markers. *Evolution*, *43*(2), 258–275.
- R_Core_Team. (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Ralls, K., Ballou, J. D., & Templeton, A. (1988). Estimates of Lethal Equivalentents and the Cost of Inbreeding in Mammals. *Conservation Biology*, *2*(2), 185–193.
- Robbins, M. M. (2009). Male Aggression against Females in Mountain Gorillas: Courtship or Coercion? In M. N. Muller & R. W. Wrangham (Eds.), *Sexual Coercion in Primates and Humans* (pp. 112–127). Cambridge, MA: Harvard Univ

Press.

- Robins, G., Pattison, P., Kalish, Y., & Lusher, D. (2007). An introduction to exponential random graph (p^*) models for social networks. *Social Networks*, 29(2), 173–191. <https://doi.org/10.1016/j.socnet.2006.08.002>
- Sakamaki, T., & Hayaki, H. (2015). Greetings and dominance. In M. Nakamura, K. Hosaka, N. Itoh, & K. Zamma (Eds.), *Mahale Chimpanzees: 50 Years of Research* (pp. 459–471). Cambridge: Cambridge University Press.
- Sandel, A. A., Reddy, R. B., & Mitani, J. C. (2016). Adolescent male chimpanzees do not form a dominance hierarchy with their peers. *Primates*, 57. <https://doi.org/10.1007/s10329-016-0553-z>
- Sargeant, B., Watson-Capps, J., Scott, E., Connor, R., & Mann, J. (2005). Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour*, 142(1), 21–44. <https://doi.org/10.1163/1568539053627712>
- Sato, Y., & Kohama, T. (2007). Post-copulatory Mounting Behavior of the West Indian Sweetpotato Weevil, *Euscepes postfasciatus* (Fairmaire) (Coleoptera: Curculionidae). *Ethology*, 113(2), 183–189. <https://doi.org/10.1111/j.1439-0310.2006.01309.x>
- Schino, G., & Aureli, F. (2009). Reciprocal Altruism in Primates: Partner Choice, Cognition, and Emotions. In *Advances in the Study of Behavior* (1st ed., Vol. 39, pp. 45–69). Elsevier Inc. [https://doi.org/10.1016/S0065-3454\(09\)39002-6](https://doi.org/10.1016/S0065-3454(09)39002-6)
- Schino, G., Scucchi, S., Maestripieri, D., & Turillazzi, P. G. (1988). Allogrooming as a Tension-Reduction Mechanism: A Behavioral Approach. *American Journal of Primatology*, 16, 43–50.
- Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20(24), 2207–10. <https://doi.org/10.1016/j.cub.2010.10.058>
- Seeman, T. E. (1996). Social ties and health: the benefits of social integration. *Annals of Epidemiology*, 6(5), 442–451. [https://doi.org/10.1016/S1047-2797\(96\)00095-6](https://doi.org/10.1016/S1047-2797(96)00095-6)
- Seltmann, A., Franz, M., Majolo, B., Qarro, M., Ostner, J., & Schülke, O. (2016). Recruitment and monitoring behaviors by leaders predict following in wild Barbary macaques (*Macaca sylvanus*). *Primate Biology*, 3(2), 23–31. <https://doi.org/10.5194/pb-3-23-2016>
- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys.

- Journal of Theoretical Biology*, 65(4), 671–98. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/406485>
- Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, 308, 541–543. <https://doi.org/10.1038/308541a0>
- Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 362(January), 539–559. <https://doi.org/10.1098/rstb.2006.1994>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science (New York, N.Y.)*, 302(5648), 1231–4. <https://doi.org/10.1126/science.1088580>
- Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61(2), 183–195. <https://doi.org/10.1007/s00265-006-0249-2>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... Cheney, D. L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings. Biological Sciences / The Royal Society*, 276(1670), 3099–104. <https://doi.org/10.1098/rspb.2009.0681>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology: CB*, 20(15), 1359–61. <https://doi.org/10.1016/j.cub.2010.05.067>
- Silk, J. B., Cheney, D., & Seyfarth, R. (2013). A Practical Guide to the Study of Social Relationships. *Evolutionary Anthropology*, 22(5), 213–225. <https://doi.org/10.1002/evan.21367>
- Smith, K. P., & Christakis, N. a. (2008). Social Networks and Health. *Annual Review of Sociology*, 34(1), 405–429. <https://doi.org/10.1146/annurev.soc.34.040507.134601>
- Smouse, P. E., Vitzthum, V. J., & Neel, J. V. (1981). The impact of random and lineal fission on the genetic divergence of small human groups: a case study among the Yanomama. *Genetics*, 98, 179–197.
- Smuts, B. B., & Smuts, R. W. (1993). Male Aggression and Sexual Coercion of Females in Nonhuman Primates and Other Mammals: Evidence and Theoretical Implications. In *Advances in the Study of Behavior*, Vol. 22 (pp. 1–63). Academic Press. Inc.
- Snijders, T. A. B. (2011). Statistical Models for Social Networks. *Annual Review of*

- Sociology*, 37(1), 131–153. <https://doi.org/10.1146/annurev.soc.012809.102709>
- Snijders, T. A. B., Bunt, G. G. van de, & Steglich, C. E. G. (2010). Introduction to stochastic actor-based models for network dynamics. *Social Networks*, 32, 44–60. <https://doi.org/10.1016/j.socnet.2009.02.004>
- Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2012). Defining Higher Levels in the Multilevel Societies of Geladas (*Theropithecus gelada*). *International Journal of Primatology*, 33(5), 1054–1068. <https://doi.org/10.1007/s10764-012-9584-5>
- Stanton, M. a, & Mann, J. (2012). Early social networks predict survival in wild bottlenose dolphins. *PloS One*, 7(10), e47508. <https://doi.org/10.1371/journal.pone.0047508>
- Stern, B. R., & Smith, D. G. (1984). Sexual behavior and paternity in three captive groups of rhesus monkeys (*macaca mulatta*). *Animal Behavior*, 32, 23–32.
- Stevens, J. R., & Hauser, M. D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, 8(2), 60–65. <https://doi.org/10.1016/j.tics.2003.12.003>
- Stevens, J. R., Volstorf, J., Schooler, L. J., & Rieskamp, J. (2010). Forgetting constrains the emergence of cooperative decision strategies. *Frontiers in Psychology*, 1(January), 235. <https://doi.org/10.3389/fpsyg.2010.00235>
- Storz, J. F. (1999). Genetic consequences of mammalian social structure. *Journal of Mammalogy*, 80(2), 553–569.
- Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, 348(6241), 1358–1361. <https://doi.org/10.1126/science.aaa5099>
- Strier, K. B. (1990). New World primates, new frontiers: Insights from the woolly spider monkey, or muriqui (*Brachyteles arachnoides*). *International Journal of Primatology*, 11(1), 7–19. <https://doi.org/10.1007/BF02193693>
- Strier, K. B., Boubli, J. P., Possamai, C. B., & Mendes, S. L. (2006). Population Demography of Northern Muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Minas Gerais, Brazil. *American Journal of Physical Anthropology*, 130, 227–237. <https://doi.org/10.1002/ajpa>
- Strier, K. B., Mendes, F. D. C., Rímoli, J., & Rímoli, A. O. (1993). Demography and Social Structure of One Group of Muriquis (*Brachyteles arachnoides*). *International Journal of Primatology*, 14(4), 513–526.

- Stumpf, R. M., & Boesch, C. (2005). Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire. *Behavioral Ecology and Sociobiology*, *57*(5), 511–524. <https://doi.org/10.1007/s00265-004-0868-4>
- Stumpf, R. M., & Boesch, C. (2006). The efficacy of female choice in chimpanzees of the Taï Forest, Côte d'Ivoire. *Behavioral Ecology and Sociobiology*, *60*(6), 749–765. <https://doi.org/10.1007/s00265-006-0219-8>
- Stumpf, R. M., & Boesch, C. (2010). Male aggression and sexual coercion in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour*, *79*(2), 333–342. <https://doi.org/10.1016/j.anbehav.2009.11.008>
- Sugiyama, Y. (1988). Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. *International Journal of Primatology*, *9*(5), 393–407. <https://doi.org/10.1007/BF02736216>
- Sugiyama, Y. (1999). Socioecological Factors of Male Chimpanzee Migration at Bossou, Guinea. *Primates*, *40*(January), 61–68.
- Sugiyama, Y. (2004). Demographic Parameters and Life History of Chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology*, *124*, 154–165. <https://doi.org/10.1002/ajpa.10345>
- Sussman, R. W. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology*, *13*(4), 395–413. <https://doi.org/10.1007/BF02547825>
- Sussman, R. W. (2013). Why the Legend of the Killer Ape Never Dies: The Enduring Power of Cultural Beliefs to Distort Our View of Human Nature. In D. Fry (Ed.), *War, Peace, and Human Nature* (pp. 97–111). New York: Oxford University Press.
- Swedell, L., & Schreier, A. (2009). Male Aggression toward Females in Hamadryas Baboons: Conditioning, Coercion, and Control. In M. N. Muller & R. W. Wrangham (Eds.), *Sexual Coercion in Primates and Humans* (pp. 244–270). Cambridge, MA: Harvard Univ Press.
- Team, R. C. (2014). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org>
- Terry, R. L. (1970). Primate grooming as a tension reduction mechanism. *The Journal of Psychology*, *76*, 129–136.
- Tokuda, M., Boubli, J. P., Mourthé, Í., Izar, P., Possamai, C. B., & Strier, K. B. (2013).

- Males Follow Females During Fissioning of a Group of Northern Muriquis. *American Journal of Primatology*, (November), 1–10.
<https://doi.org/10.1002/ajp.22244>
- Trivers, R. L. (1972). Parental Investment and Sexual Selection. In *Sexual selection and the descent of man 1871-1971* (pp. 136–207). Chicago: Aldine Publishing Co.
- van Hooff, J. A. R. A. M., & van Schaik, C. P. (1994). Male Bonds: Affiliative Relationships Among Nonhuman Primate Males. *Behaviour*, 130(3), 309–337.
<https://doi.org/10.1163/156853994X00587>
- Van Horn, R. C., Buchan, J. C., Altmann, J., & Alberts, S. C. (2007). Divided destinies: Group choice by female savannah baboons during social group fission. *Behavioral Ecology and Sociobiology*, 61(12), 1823–1837. <https://doi.org/10.1007/s00265-007-0415-1>
- van Lawick-Goodall, J. (1975). The Behaviour of the Chimpanzee. In G. Kurth (Ed.), *Hominisation und Verhalten/ Hominisation and Behavior* (pp. 74–136). Stuttgart: Gustav Fischer Verlag.
- Van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, 1(3), 161–311.
[https://doi.org/10.1016/S0066-1856\(68\)80003-2](https://doi.org/10.1016/S0066-1856(68)80003-2)
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen & R. Foley (Eds.), *Comparative Socioecology of Mammals and Man* (pp. 195–218). Oxford: Blackwell Scientific.
- van Schaik, C. P., & Kappeler, P. M. (1997). Infanticide risk and the evolution of male-female association in primates. *Proceedings. Biological Sciences / The Royal Society*, 264(1388), 1687–1694. <https://doi.org/10.1098/rspb.1997.0234>
- van Schaik, C. P., & Kappeler, P. M. (2006). Cooperation in primates and humans: closing the gap. In P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in Primates and Humans: Mechanisms and Evolution I* (pp. 3–24). Berlin: Springer.
- VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, 77(4), 949–954. <https://doi.org/10.1016/j.anbehav.2008.12.028>
- Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and Relatedness in Wild Chimpanzee Communities. *Proceedings of the National Academy of Sciences of the United States of America*, 98(23), 12890–12895.
- Voelkl, B., & Kasper, C. (2009). Social structure of primate interaction networks

- facilitates the emergence of cooperation. *Biology Letters*, 5, 462–464.
<https://doi.org/10.1098/rsbl.2009.0204>
- Wakefield, M. L. (2008). Grouping patterns and competition among female Pan troglodytes schweinfurthii at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, 29(4), 907–929. <https://doi.org/10.1007/s10764-008-9280-7>
- Walker, K. K., Rudicell, R. S., Li, Y., Hahn, B. H., Wroblewski, E., & Pusey, A. E. (2017). Chimpanzees breed with genetically dissimilar mates. *Royal Society Open Science*, 4(1), 160422. <https://doi.org/10.1098/rsos.160422>
- Walker, R. S., & Hill, K. R. (2014). Causes, Consequences, and Kin Bias of Human Group Fissions. *Human Nature*, 25(4), 465–475. <https://doi.org/10.1007/s12110-014-9209-0>
- Wallace, R. B. (2008). Towing the party line: territoriality, risky boundaries and male group size in spider monkey fission-fusion societies. *American Journal of Primatology*, 70(3), 271–81. <https://doi.org/10.1002/ajp.20484>
- Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications* (Vol. 8). Cambridge University Press.
- Waterman, J. M. (2006). Delayed maturity, group fission and the limits of group size in female Cape ground squirrels (Sciuridae: Xerus inauris). *Journal of Zoology*, 256(1), 113–120. <https://doi.org/10.1017/S0952836902000146>
- Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, 44, 43–55.
- Watts, D. P. (2000). Grooming between male chimpanzees at Ngogo, Kibale National Park, Uganda. II. Male rank and priority of access to partners. *International Journal of Primatology*, 21(2), 211–238.
- Watts, D. P. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, 139(2), 343–370.
<https://doi.org/10.1163/156853902760102708>
- Watts, D. P. (2006). Conflict Resolution in Chimpanzees and the Valuable-relationships Hypothesis. *International Journal of Primatology*, 27(5), 1337–1364.
<https://doi.org/10.1007/s10764-006-9081-9>
- Watts, D. P. (2010). Dominance, Power, and Politics in Nonhuman and Human Primates. In P. M. Kappeler & J. B. Silk (Eds.), *Mind the Gap* (pp. 109–138). Berlin, Heidelberg: Springer Verlag.

- Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*, 299–327.
- Whitehead, H., & Lusseau, D. (2012). Animal social networks as substrate for cultural behavioural diversity. *Journal of Theoretical Biology*, *294*, 19–28.
<https://doi.org/10.1016/j.jtbi.2011.10.025>
- Whitlock, M. C., & McCauley, D. E. (1990). Some population genetic consequences of colony formation and extinction: Genetic correlation within founding groups. *Evolution*, *44*(7), 1717–1724. <https://doi.org/10.2307/2409501>
- Widdig, A., Nürnberg, P., Bercovitch, F. B., Trefilov, A., Berard, J. B., Kessler, M. J., ... Krawczak, M. (2006). Consequences of group fission for the patterns of relatedness among rhesus macaques. *Molecular Ecology*, *15*(12), 3825–32.
<https://doi.org/10.1111/j.1365-294X.2006.03039.x>
- Wilkinson, G. S. (1985). The social organization of the common vampire bat I: Pattern and cause of association. *Behavioral Ecology and Sociobiology*, *17*, 111–121.
- Williams, J. M., Oehlert, G. W., Carlis, J. V., & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? *Animal Behaviour*, *68*(3), 523–532.
<https://doi.org/10.1016/j.anbehav.2003.09.015>
- Williams, J. M., Pusey, A. E., Carlis, J. V., Farm, B. P., & Goodall, J. (2002). Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Animal Behaviour*, *63*, 347–360. <https://doi.org/10.1006/anbe.2001.1916>
- Wilson, M. L. (2012). Long-Term Studies of the Chimpanzees of Gombe National Park, Tanzania. In P. M. Kappeler & D. P. Watts (Eds.), *Long-Term Field Studies of Primates* (pp. 357–384). Berlin, Heidelberg: Springer Berlin Heidelberg.
<https://doi.org/10.1007/978-3-642-22514-7>
- 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*, 414–417.
<https://doi.org/10.1038/nature13727>
- Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T., & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature Communications*, *7*, 13361. <https://doi.org/10.1038/ncomms13361>
- 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.

<https://doi.org/10.1007/s00265-013-1534-5>

- Wrangham, R. W. (1974). Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour*, 22(1), 83–93. [https://doi.org/10.1016/S0003-3472\(74\)80056-4](https://doi.org/10.1016/S0003-3472(74)80056-4)
- Wrangham, R. W. (1979). On the evolution of ape social systems. *Social Science Information*, 18(3), 336–368.
- Wrangham, R. W. (1999). Evolution of Coalitionary Killing. *Yearbook of Physical Anthropology*, 42, 1–30.
- Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In P. M. Kappeler (Ed.), *Primate males: causes and consequences of variation in group composition* (pp. 248–258). Cambridge University Press.
- Wrangham, R. W. (2002). The cost of sexual attraction : is there a trade-off in female Pan between sex appeal and received coercion ? In C. Boesch, G. Hohmann, & L. Marchant (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos* (pp. 204–216). Cambridge University Press.
- Wrangham, R. W., Gittleman, J. L., & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral Ecology and Sociobiology*, 32, 199–209.
- Wrangham, R. W., & Peterson, D. (1996). *Demonic Males*. New York: Houghton Mifflin.
- Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility. Supplement, Suppl 28*, 13–31. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/6934308>
- Wrangham, R. W., Wilson, M. L., & Muller, M. N. (2006). Comparative rates of violence in chimpanzees and humans. *Primates; Journal of Primatology*, 47(1), 14–26. <https://doi.org/10.1007/s10329-005-0140-1>
- 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. <https://doi.org/10.1016/j.anbehav.2008.12.014>
- Yee, J. R., Cavigelli, S. a, Delgado, B., & McClintock, M. K. (2008). Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary

tumors and lifespan. *Psychosomatic Medicine*, 70(9), 1050–9.
<https://doi.org/10.1097/PSY.0b013e31818425fb>

Zachary, W. W. (1977). An Information Flow Model for Conflict and Fission in Small Groups. *Journal of Anthropological Research*, 33, 452–473.
<https://doi.org/10.2307/3629752>

Biography

Joseph T. Feldblum was born in Durham, North Carolina on August 9, 1986 to Tolly Boatwright and Paul Feldblum. He learned to navigate the academy from his mother, a professor in the department of Classical Studies at Duke University, to love science from his father, an epidemiologist at Family Health International, and to schmooze from his brother, Sammy Feldblum, a well-known bon vivant and burgeoning journalist. Feldblum earned a Bachelor of Arts from Wesleyan University in 2008, majoring in psychology and Spanish literature. In 2014 Feldblum and coauthors published “Sexually coercive male chimpanzees sire more offspring” in the journal *Current Biology* (Vol. 24). Feldblum is a Graduate Research Fellow of the National Science Foundation and a graduate fellow at the Kenan Institute for Ethics at Duke University, and has received grants from the L. S. B. Leakey Foundation, Conservation International, and numerous grants from Duke University.