Social Relationships in Male Chimpanzees:

Form, Function, and Development

by

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ABSTRACT

Understanding the evolution of cooperation is a central goal in animal behavior research. In several animal taxa, socioecological environments that promote frequent interaction and social tolerance have favored the evolution of strong, equitable, and enduring social bonds, which facilitate cooperation and confer fitness benefits. Among males, strong bonds are believed to have evolved in the context of long-term alliances that help individuals compete for dominance status and mating access, but it remains unclear in some species what factors predict the strength and quality of bonds and how sociality relates to adaptive outcomes. To fill these gaps, this dissertation presents three studies of male chimpanzees at Gombe National Park, Tanzania, addressing the form, function, and development of male social relationships. Maternal brothers who were close in age formed the strongest bonds, strong bonds were associated with more reciprocal grooming relationships, and the strength of bonds were stable for an average of two years, while lasting up to 13 years. For other males, similarity in age and rank had negligible effects on bond strength, suggesting that bond strength results from a more complex process than a simple accounting of basic characteristics. Additionally, these social bonds, identified using both association in small groups and grooming activity, showed positive relationships with changes in dominance. In combination with prior studies, these results suggest that having strong bonds is a valuable strategy for achieving higher rank and, ultimately, increased reproductive success. Lastly, immature males who associated more with particular adult males while growing up were more likely to both associate and groom with those same males after entering adulthood. By contrast, association rates among immature male peers were not correlated with bond strength as adults. These findings suggest that the persistence of social relationships beyond those between mothers and offspring are more likely to evolve in long-lived species where young males enter adult hierarchies comprised of stronger or more socially experienced competitors. Overall, these studies reinforce the notion that social bonds are a chimpanzee universal, fill in gaps about the relationship between sociality and fitness, and emphasize the utility of a prolonged immature period.

DEDICATION

To my younger self,
who made me promise
that I would walk with chimpanzees

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Among chimpanzees, the act of creation and child-rearing is largely an individual effort by mothers. Dissertations, however, are a group effort, and this one is no exception.

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CHAPTER 1

INTRODUCTION

Understanding the evolution of cooperation is a central goal in animal behavior research (Dugatkin, 2002; Silk, 2005). In several animal taxa, socioecological environments that promote frequent interaction and social tolerance have favored the evolution of strong, equitable, and enduring social bonds, which facilitate cooperation and confer fitness benefits (Ostner & Schulke, 2018; Seyfarth & Cheney, 2012; Silk, 2007). Among males, strong bonds are believed to have evolved in the context of long-term alliances that help individuals compete against other males in their social group for dominance status and mating access (Ostner & Schülke, 2014), but it remains unclear in some species what factors predict the strength and quality of bonds and how sociality relates to adaptive outcomes. To better understand the evolution of social bonds and cooperation, this dissertation presents three studies of male chimpanzees at Gombe National Park, Tanzania, each addressing social relationships from a different perspective: (1) form, (2) function, and (3) development. Additionally, by studying social relationships among one of our two closest living ape relatives, we can provide context and unearth clues about the evolution and origins of human friendship (Wrangham & Pilbeam, 2002; Muller, Wrangham, & Pilbeam, 2017).

In Chapter 2, I characterize variation in the strength and quality of social bonds in adult male chimpanzees over the course of 38 years. In most species, kinship is the main predictor of bond strength and quality (Seyfarth & Cheney, 2012), but it does not sufficiently explain the patterns of partner choice that are observed among adult male chimpanzees (Langergraber et al., 2007). Instead, most bonds and cooperative interactions arise among unrelated individuals (Langergraber et al., 2007; Mitani, 2009a). Chimpanzees thus provide an opportunity to investigate what factors contribute to variation in partner choice when the influence of kinship is limited. In addition, to better understand the value of maintaining close social relationships in chimpanzees, I also examined the stability of social bonds from one year to the next as well as the total number of years that dyads continuously formed strong bonds.

In Chapter 3, using 37 years of data, I test the hypothesis that same-sex social bonds in adult male chimpanzees predict changes in dominance strength. Several studies of wild chimpanzees have found that higher ranking males achieve greater reproductive success (Boesch et al., 2006; Inoue et al., 2008; Langergraber et al., 2013; Newton-Fisher et al., 2010; Wroblewski et al., 2009), but no study has demonstrated a link between social bonds and dominance trajectories. At Gombe, previous studies have documented well-differentiated social relationships among males (Chapter 1; Goodall, 1986), identified correlations between position in a coalitionary network and both paternity success and rank change (Gilby et al., 2013), and found that high rank and alpha status correlate with paternity success (Feldblum et al., under review; Wroblewski et al., 2009). This study fills a gap in our understanding of how social bonds relate to fitness in male chimpanzees by assessing whether patterns of association and grooming, two behaviors involved in bond formation and maintenance, predict changes in dominance strength.

In Chapter 4, using 46 years of data, I investigate the effect of early life social experiences on adult male social bonds in wild chimpanzees. Although much is known about the form and function of mammalian social bonds, the role of early life social experiences in the development of bonds is poorly studied. Few studies have examined whether social relationships during infancy and juvenility (aside from those between mothers and offspring) persist into adulthood. Here, I examined whether maternal association patterns with adult males during an offspring's infancy and juvenility predict the strength of the offspring's social bonds with the same partners during adulthood. Likewise, I investigated whether maternal associations with the mothers of other immature males, which create opportunities for male peers to interact, predict the strength of adult male bonds among peers.

In the Conclusion, I summarize the results, discuss their implications, and consider questions that warrant further study.

CHAPTER 2[1]

SOCIAL RELATIONSHIPS AMONG ADULT MALE CHIMPANZEES: VARIATION IN THE STRENGTH AND QUALITY OF SOCIAL BONDS

2.1 Abstract

Socioecological environments that promote frequent interaction and social tolerance have favored the evolution of strong and equitable social bonds, which facilitate cooperation and confer fitness benefits. In most species, kinship is the primary predictor of bond strength and quality, but it does not adequately explain partner choice among adult male chimpanzees. Instead, most bonds and cooperative interactions occur among unrelated individuals, likely because of a lack of brothers among available partners. To identify what factors drive partner choice when kinship does not, I investigated the strength and quality of social bonds among adult male chimpanzees (N = 26) at Gombe National Park, Tanzania. Maternal brothers, when present, formed stronger bonds than other dyads, and maternal brothers who were close in age or rank formed the strongest bonds. Among dyads that were not maternal brothers, however, the strength of social bonds was not associated with either age difference or rank difference. Additionally, dyads with stronger bonds groomed more equitably than other dyads, as did maternal brothers and dyads close in rank. Bonds were stable, community-wide, for two years on average, while lasting up to 13 years. Nevertheless, there remains no clear-cut explanation for partner choice among male chimpanzees. Demographic constraints limit the impact of kinship, and the effects of age and rank difference are small or nonexistent, suggesting that bond

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strength results from a more complex process than a simple accounting of basic characteristics. Instead, dyads may possess some distinct quality that engenders strength and stability, such as compatible personalities.

2.2 Introduction

In several animal taxa, socioecological environments that promote frequent interaction and social tolerance have favored the evolution of strong, equitable, and enduring social bonds, which facilitate cooperation and confer fitness benefits (reviewed in: Hruschka & Silk, 2017; Massen et al., 2010; Seyfarth & Cheney, 2012; Silk, 2007). For example, same-sex social bonds – typically measured by the frequency or duration of friendly interactions – are linked to cooperation in male macaques (*Macaca anamensis, M. sylvanus*) (Berghänel et al., 2011; Schülke et al., 2010), female spotted hyenas (*Crocuta crocuta*) (Smith et al., 2011), male bottlenose dolphins (*Tursiops* sp.) (Connor et al., 2001), and male chimpanzees (*Pan troglodytes*) (Mitani, 2006; Samuni et al., 2018; Watts, 2002; reviewed in: Mitani, 2009b). Furthermore, strong social bonds are associated with increased lifespans in female baboons (*Papio cynocephalus* and *P. ursinus*) (Archie et al., 2014; Silk et al., 2010b) and higher infant survival in feral horses (*Equus caballus*) (Cameron et al., 2009), bottlenose dolphins (*Tursiops* sp.) (Frère et al., 2010), and baboons (*P. cynocephalus* and *P. ursinus*) (Cheney et al., 2016; Silk et al., 2003, 2009). Among males, strong bonds are believed to have evolved in the context of long-term alliances that help individuals compete against other males in their social group for dominance status and mating access (Connor et al,. 2001; Schülke et al., 2010; Wiszniewski et al., 2012; reviewed in: Ostner & Schülke, 2014).

Substantial variation exists in the degree to which pairs of animals in multi-male, multi-female social groups form bonds and cooperate (Seyfarth & Cheney, 2012). All else equal, kin selection theory (Hamilton, 1964) predicts that partner choice will be based on the degree of relatedness. Because of the inclusive fitness benefits, close relatives will form stronger bonds and be more likely to cooperate than other dyads (Silk, 2002; Smith, 2014). According to this theory, however, relationships among kin may be more one-sided or unequal than those among non-kin because kin receive indirect fitness benefits even if altruistic behavior is not reciprocated. Maternal kin typically cooperate more because they are easier to recognize than paternal relatives, but in species with high male reproductive skew, age similarity can function as a form of paternal kin recognition (Altmann, 1979). In species where paternal kinship does not explain patterns of cooperation, such as chimpanzees (Langergraber et al., 2007), peers may still represent attractive social partners due to greater familiarity and shared interests (Gerber et al., 2020; Mitani, Watts, Pepper, et al., 2002). Finally, in species where allogrooming is a common form of cooperative behavior, as in many primates, rank similarity may also influence partner choice (de Waal, 1991; de Waal & Luttrell, 1986; Schino, 2001; Seyfarth, 1977; Watts, 2000b). If individuals compete for high-ranking, valuable partners, then males that are more similar in rank should form stronger and more equitable bonds. Alternatively, if individuals of similar rank are more likely to compete with one another, then they should form weaker social bonds. Lower-ranking individuals may also exchange grooming with high-ranking individuals for tolerance, agonistic support, or mating opportunities (Borgeaud & Bshary, 2015; Kaburu & Newton-Fisher, 2015; Tiddi et al., 2011), resulting in inequitable grooming patterns.

Empirically, several factors are associated with bond strength and quality among same-sex dyads, including kinship and similarity in age and rank (reviewed in: Seyfarth & Cheney, 2012). In female philopatric species, including baboons (*P. cynocephalus* and *P. ursinus*) (Silk et al., 2010a, 2012; Silk, Altmann, et al., 2006) and spotted hyenas (*C. crocuta*) (Smith et al., 2010, 2011), females form the strongest and most equitable relationships with maternal kin. In other species, however, kinship provides an incomplete explanation for partner choice in social bonds and cooperation. In the Ngogo chimpanzee community, for example, although maternal brothers do form stronger and more equitable social bonds than other dyads, most strong bonds are formed between dyads that are not closely related (Langergraber et al., 2007; Mitani, 2009a). In this respect, male-male bonds in chimpanzees bear a striking resemblance to human friendships, in which strong and enduring relationships among non-kin are widespread (Hruschka, 2010). There are multiple explanations for the limited role of kinship in bond formation. In agonistic contexts, the inclusive fitness benefits of nepotism may be outweighed by the greater fitness benefit of selecting a partner based on competence (Chapais, 2006). Additionally, in species with long interbirth intervals, the likelihood that an individual has a same-sex sibling that survives to adulthood, can be identified as kin, and is of high competitive quality, is low. In these contexts, other factors may therefore have more impact on partner choice, including age or rank similarity (Mitani, Watts, Pepper, et al., 2002; Gerber et al., 2020) or greater familiarity (Pusey, 1990; Mitani, Watts, Pepper, et al., 2002; Rosenbaum et al., 2015; Gerber et al., 2020).

Adult male chimpanzees remain in their natal communities for life, are highly gregarious, and form some of the strongest and most stable social bonds among mammals

(Goodall, 1986; Boesch & Boesch-Achermann, 2000; Gilby & Wrangham, 2008; Mitani, 2009a, b). Male bonds manifest in a variety of social contexts, including association within the same subgroup or party (Gilby & Wrangham, 2008; Newton-Fisher, 1999; Pepper et al., 1999; Surbeck, Girard-Buttoz, et al., 2017), maintenance of close proximity (Gilby & Wrangham, 2008; Mitani, Watts, Pepper, et al., 2002), grooming (Arnold & Whiten, 2003; Gomes et al., 2009; Newton-Fisher & Lee, 2011; Watts, 2000a, 2000b), coalitionary aggression (Gilby et al., 2013; Muller & Mitani, 2005), meat sharing (Mitani, Watts, Pepper, et al., 2002; Samuni et al., 2018), and territorial boundary patrols (Watts & Mitani, 2001). Males are also more likely to reconcile with close social partners (Preis et al., 2018), and bystanders are more likely to intervene in a grooming bout when a close partner is grooming another individual (Mielke et al., 2017).

Male-male cooperation is likely to have important fitness consequences for males. For example, male chimpanzees form coalitions in agonistic contests that play an important role in the acquisition of high rank (Gilby et al., 2013; Goodall, 1986; Mitani, 2009b; Muller & Mitani, 2005), and high rank enhances reproductive success in every community studied (Boesch et al., 2006; Inoue et al., 2008; Langergraber et al., 2013; Newton-Fisher et al., 2010; Wroblewski et al., 2009). In addition, Watts (1998) demonstrated that cooperative mate guarding increased male mating success at Ngogo, and rates of coalition formation and grooming with alpha males, respectively, were positively associated with mating success in chimpanzees at Kanyawara (Duffy et al., 2007) and Gombe (Bray et al., 2016).

Because most strong bonds and cooperative interactions extend beyond close kin in male chimpanzees, I can investigate what factors contribute to variation in partner choice when kinship does not. Here, I examine the strength and quality of male chimpanzee social bonds at Gombe National Park, Tanzania. To better understand the importance and nature of social bonds in this species, I also examine bond stability and duration.

2.3 Methods

2.3.1 *Study Site, Subjects, and Data Collection*

I studied chimpanzees (*P. t. schweinfurthii*) from the Kasekela community in Gombe National Park, Tanzania. The park consists of 35 km^2 of evergreen riverine forest, deciduous woodland, and grassland (Clutton-Brock & Gillett, 1979). Chimpanzees live in large multi-male, multi-female social groups, called communities, that typically associate in subgroups, or parties, that frequently change in size and composition (Boesch & Boesch-Achermann, 2000; Goodall, 1986). The Kasekela community has been studied continuously since 1960, and it became fully habituated in 1966 through banana provisioning at a feeding station (Wilson, 2012). Feeding continued at low levels until 2000 when it ceased entirely (Wilson, 2012). Since 1973, Tanzanian field assistants have conducted full-day focal observations of Kasekela chimpanzees (Altmann, 1974; Wilson, 2012). Teams of two observers follow each individual that travels independently of its mother approximately once per month. During a focal follow, one observer records when individuals join and leave the focal chimpanzee's party. Two individuals are considered to have 'arrived' together if they either (i) are present in the party at the start of a focal follow or (ii) join a party within five minutes of each other. A second observer records a continuous narrative of the behavior of the focal chimpanzee and conspicuous non-focal activities such as submissive pant-grunt vocalizations. It was not possible to record data blindly because this study involved focal animals in the field. A relational database, including both behavioral and demographic data, is maintained by the Gombe Research Consortium and coordinated by the Institute of Human Origins at Arizona State University.

2.3.2 *Analyses*

I used behavioral data from 1978 to 2015, during which all necessary data were available. Data on paternal relatedness were not available for most dyads and were therefore not included in any analysis. I classified males as adults if they were ≥ 16 years old (Goodall, 1986; Mitani, 2009a; Sandel et al., 2016); this age generally corresponds to physical (full body size) and social maturity (entry into the adult male dominance hierarchy). In total, I examined social bonds among 26 individual adult males and 157 dyads. In any given year, the number of adult males ranged from 4 to 11, corresponding to 6 to 55 dyads. The median number of years that dyads co-resided in the community was 6 (range: 1 – 24; $N = 157$).

The birthdates of 19 males born in the Kasekela community after the study began were estimated based on both their size and appearance when first observed as well as the dates of previous sightings of the mother without the infant (Strier et al., 2010). The median difference between the minimum and maximum birthdates was 7 days (Mean ± SD = 8.3 ± 9.2, $N = 19$). For the seven remaining males, minimum and maximum birthdates were estimated based on morphological characteristics and familial relationships; unsurprisingly, the median difference between the minimum and maximum birthdates was larger (Mean ± SD = 678 ± 390 days, $N = 7$).

(i) Bond Strength

To assess the strength of male-male ("male", hereafter) social bonds, I calculated two annual indices, one based on party-level association and one on grooming, both of which I define below. These behaviors are standard for assessing adult male social bonds in chimpanzees (Gilby & Wrangham, 2008; Goodall, 1986; Mitani, 2009b; Newton-Fisher, 1999; Samuni et al., 2018). By analyzing both behaviors separately, I could examine whether there were differences in the factors influencing each behavior and explore the impact of methodological decisions, allowing for easier comparisons to past and future studies.

As a measure of party-level association, I calculated an annual Dyadic Association Index based on joint arrivals into a party (see above) (Foerster et al., 2015; Williams et al., 2002). These data accrue throughout the entire day, including instances when the focal individual joins another party and when other individuals join a party with the focal individual. To avoid non-independent arrivals resulting from individuals leaving and re-joining a party throughout the day, I included only the earliest arrival of an individual per day. Because associations of large numbers of individuals are more likely to reflect grouping for reasons other than social preference, such as a high-quality food resource or a female in estrous (Matsumoto-Oda et al., 1998; Mitani, Watts, & Lwanga, 2002), I further restricted the data to include only arrivals of four adult individuals or fewer (to be included, females had to be ≥ 15 years old, the average age at first birth at

Gombe: Walker et al., 2018). Even for highly gregarious males who prefer to spend time in large groups, this latter criterion identifies their strongest partner preferences. Finally, I eliminated all dyads from the analysis for which at least one of the members had 20 or fewer arrivals in a given year, which eliminated biases from indices that would otherwise have been based on a small number of data points (Foerster et al., 2015). In essence, this index estimates how often pairs of adult males spent time together in parties, even though observers may not have been present to witness social interactions. Note that this index is also positively correlated with association indices based on the proportion of time spent together. I calculate the association indices for each dyad as follows:

$$\frac{J_{i,j}}{A_i + A_j - J_{i,j}}$$

where $J_{i,j}$ is the number of joint arrivals for each dyad, A_i is the total number of arrivals of male i, and A_j is the total number of arrivals of male j (Cairns & Schwager, 1987). In total, my analyses were based on 11,538 joint arrivals. The annual number of joint arrivals between two individuals ranged from 0 to 50 (Mean ± SD = 5.2 ± 5.0). Finally, because annual association indices were calculated from the perspective of each adult male, I averaged these scores within each dyad (Pearson's correlation: $r = 0.994$, $N = 157$ dyads, $P < 0.0001$).

I also calculated an annual Dyadic Grooming Index: the amount of time a dyad was observed grooming divided by the total observation time in which the members were both present in the same party and either member was the focal subject (Machanda et al., 2013). This index measures the tendency for two individuals to groom, given that they are together in a party. I limited analyses to dyads that were together in parties in any given year for ≥ 1800 minutes. This ensured that data would not be biased by dyads that were rarely together but groomed frequently when they were.

In some years, observers recorded grooming during instantaneous point samples (conducted every five minutes during a grooming session), whereas in other years grooming was recorded ad libitum as part of the continuous narrative. For years when both instantaneous point sampling and ad libitum sampling were available, the two methods produced highly correlated grooming indices (Pearson's correlation: $r = 0.79$, $N = 638$ grooming indices, $P < 0.0001$). Therefore, the grooming index was based on instantaneous point samples when they were available, and ad libitum when they were not. Because the duration of some grooming bouts in the continuous narrative notes were uncertain, I only included those for which the observers had recorded precise start and end times (76.3%, $N = 7271$ bouts).

(ii) Grooming Equality

To measure how balanced grooming relationships were within dyads, I calculated an annual Grooming Equality Index. This index has been previously used in studies of chimpanzees and other primates to assess the quality of male social bonds (Mitani, 2009a; Silk, Alberts, et al., 2006) and is calculated as follows:

$$1 - \left\| \left[\frac{(G_{x\rightarrow y} - G_{y\rightarrow x})}{(G_{x\leftrightarrow y})} \right] \right\|$$

where $G_{x\rightarrow y}$ is the amount of time that x grooms y, $G_{y\rightarrow x}$ is the amount of time y grooms x, and $G_{x\leftrightarrow y}$ is the total amount of time xy spends grooming. Mutual grooming was included as grooming both given and received. The Grooming Equality Index equals 1 when the amount of grooming given and received is equal within a dyad and 0 when grooming is completely unidirectional. To avoid biases that might result from individuals that rarely groomed, I removed 324 dyad-years that groomed for < 11 minutes. I chose this cutoff before running my models based on a visual inspection of a histogram of the data. There were a substantial number of dyads that groomed between 0 and 10 minutes (e.g., many more than dyads that groomed between 10 and 20 minutes) but no well-defined cutoff above 10 minutes. All analyses involving this index were restricted to the remaining dyads (*N* = 702 dyad-years).

(iii) Bond Stability

I investigated bond stability using statistical models based on the bond strength indices (see below). In addition, I ordered – on an annual basis – the bonds of each male (from strongest to weakest) according to the value of each annual bond strength index. To evaluate the stability of each male's strongest and weakest relationships, I then calculated a Partner Stability Index (Silk et al., 2012, 2013) using the following formula:

$$\frac{NS - U}{NS - S}$$

where N is the number of years in which partner orders were evaluated, S is the number of ordered slots being evaluated (e.g. if calculating the stability of a male's top two partners, this value would be two), and U is the observed number of unique partners. The value of the Partner Stability Index varies from 1 (males that had the same partners in each year) to 0 (males that had a completely different set of partners in each year). I calculated four indices for each individual male to assess the stability of his strongest relationship, strongest two relationships, weakest relationship, and weakest two relationships. Using this index, I was able to (a) examine partner stability for males who did not have strong bonds relative to the rest of the community and (b) investigate whether males had more stable relationships with partners who they preferred compared to partners they avoided, as is found among female baboons (Silk et al., 2012).

(iv) Bond Duration

For each year that dyads resided together in the community as adults, I first classified them as having a “very strong bond” or not, based on the dyad's bond strength index being at least one standard deviation above the average for that year. I did this separately for the annual association and grooming indices. Of the 26 males in the study, only one never had a very strong association bond, and he was in the dataset for just one year. Four males never had a very strong grooming bond; of these males, three were in the dataset for a year and the fourth for three years.

To measure the bond duration of each dyad, I calculated the maximum number of consecutive years that a dyad formed a very strong bond, allowing for one-year gaps (Mitani, 2009a; Silk, Alberts, et al., 2006). For example, if a dyad formed a very strong bond for two consecutive years, not in a third year, and then for another year afterwards, they would be given a bond duration of four years. Note that if dyads did not meet inclusion criteria in a given year (i.e., if the dyad was not together in the same party for ≥ 1800 minutes, or if either member had 20 or fewer individual arrivals), the dyad was included in the bond duration analysis, but I classified the dyad as not having a very strong bond in that year.

(iv) Dominance Rank

I identified all pant-grunt vocalizations (formal signals of submission in chimpanzees: Bygott, 1979; Goodall, 1986) between males that were observed at the feeding station or during focal follows. These interactions were used to calculate Elo ratings (Albers & de Vries, 2001), which estimate a subject's dominance rank on any given date while accounting for demographic changes and missing data (Neumann et al., 2011). To calculate Elo scores on each day of the study period, I used a maximum-likelihood implementation of the Elo score method using the 'EloOptimized' package (Feldblum et al., 2018; Foerster et al., 2016). To estimate annual dominance rank scores for each male, I calculated mean daily Elo scores for each year.

2.3.3 *Statistical Analyses*

All statistical models in this study had a non-directional dyadic response variable, with both individuals and dyads repeated across rows in the data. Because the individual identities of the members of each dyad were stored in separate columns, traditional statistical methods would estimate two discrete varying effects, one for each column. To solve this problem, I followed a method that used multiple indexing notation to estimate a single varying intercept from the two columns of individual identities (for details, see Silk et al., 2017). A separate varying intercept was specified for the dyad. I also explicitly specified the mathematical structure of all statistical models and made this code available (https://github.com/joelbray/form-male-bonds).

I fit all models using Hamilton Markov chain Monte Carlo (MCMC) with r-STAN v.2.19.13 (Stan Development Team, 2020) in R v.3.6.2 (R Core Team, 2019), using the map2stan function in the ‘rethinking’ package (McElreath, 2019). When these models are executed, they produce a specified number of estimates for the value of each parameter, which together create a posterior distribution for each parameter. By taking the mean, median, or standard deviation of these values, I can estimate the posterior mean, posterior median, and posterior standard deviation for each parameter. I can also estimate a highest posterior density interval, which is the narrowest credible interval (CI) containing a specified percentage of estimates. In this study, I used 89% credible intervals wherever applicable. To make statistical inferences, I used both tables of parameter estimates and plots of the posterior predictions. Although the sign and magnitude of the parameter estimates provides some information, plotting model predictions is particularly helpful for interpreting effects from mixture models that combine multiple distributions (see below).

In all models, I used weakly informative priors for the fixed effects (Gelman et al., 2008). Weakly informative priors constrain parameter estimates to biologically plausible values, while allowing the information in the data to dominate information in the prior. Because I standardized all numeric predictor variables, I set the means of the priors to 0 and the standard deviations to 2. To verify that the models were insensitive to these chosen priors, however, I ran a series of models with both relatively flat priors and more informative priors, and the results were unaffected. I used exponential priors for most variance components and shape and scale parameters, which induce conservatism in estimates and helps models to converge (McElreath, 2016, p. 363-364). I also used non-centered parameterization (i.e., a standardized adaptive prior) for all varying effects, which makes MCMC algorithms sample more efficiently by setting the means to 0 and the standard deviations to 1 (McElreath, 2016, p. 405-408).

I evaluated the quality of my models by visually inspecting the trace plots (McElreath, 2016, p. 253-254) and examining two numerical diagnostics. The first diagnostic, effective sample size, estimates the number of independent draws from the posterior distribution. Effective sample sizes that are substantially lower than the number of iterations in the chains indicate that the models are inefficient (McElreath, 2016, p. 257). The second, the Gelman-Rubin convergence diagnostic (Rhat), evaluates the convergence of different chains (Gelman & Rubin, 1992). Rhat values that deviate from 1.00 are cause for concern (McElreath, 2016, p. 257). Here, all Rhat values were 1.00 and the number of effective sample sizes for all predictor variables were above 2000. I report both model diagnostics in Table S2.1 (Appendix A).

In all models, I standardized (z-transformed) numeric predictor variables by centering and scaling the data (Schielzeth, 2010). To center the data, I subtracted the variable mean from each value, resulting in a mean of zero. I then scaled the data by dividing the newly centered data by its standard deviation. When data are standardized in this manner, coefficients indicate the change in the response variable associated with an increase in one standard deviation of the predictor variable (Bring, 1994; McElreath, 2016, p. 111). This procedure also improves how well the model is fit to the data, increasing the accuracy of parameter estimates (McElreath, 2016, p. 111). Note that because the range of Elo ratings changes over time, I standardized dominance rank variables within years. Binary variables were not standardized.

(i) Bond Strength

I used a hierarchical zero-augmented gamma model, which combines a Bernoulli and gamma distribution. The Bernoulli component uses a logit link and estimates p, the probability of observing an outcome of 0. For all outcomes > 0, the gamma component estimates the mean, λ, and a shape parameter, k. The joint likelihood is calculated by multiplying the likelihoods of each distribution together and converting them to a real scale using their link functions (for more detail, see Silk et al., 2017). Negative regression coefficients in the Bernoulli component (β_z) signify a lower probability of observing an outcome of zero, while positive regression coefficients in the gamma component (β_g) signify larger average outcomes.

I fit statistical models to both bond strength indices. The annual predictor variables were age and rank for each individual, age difference, rank difference, and maternal kinship (whether the members of a dyad were maternal brothers). I also included interactions between maternal kinship and both age difference and rank difference.

I specified varying intercepts for subject identity, dyad identity, and year. Because individual age, individual rank, and dyadic rank difference all varied across years, and their effects on bond strength might vary by individual and dyad, I also specified varying slopes for these effects.

The minimum age difference among maternal brothers (3.29 years) was naturally higher than the minimum age difference among other dyads (0.15 years), so I also ran a series of models that excluded all dyads who were less than 3.29 years apart. The results were unaffected, and therefore I report only results from the full dataset.

(ii) Grooming Equality

I fit models to grooming equality data using a beta distribution. Because beta distributions require values between 0 and 1 ($0 < x < 1$), excluding zero and one, I transformed the grooming equality index: I subtracted 0.5 from each value, multiplied by 0.999, and then added 0.5 back to all values. The new range was 0.0005 to 0.9995, which satisfied the conditions of the beta distribution without meaningfully changing the values or distribution of the raw data.

The response variable was the annual Grooming Equality Index. The predictor variables included age and rank for each individual, age difference, rank difference, maternal kinship, bond strength, and the number of males in the community. I examined models with interactions between maternal kinship and both age and rank difference, but these models produced worse fits to the data so both interactions were removed from the final models.

As in previous models, I specified varying effects for subject identity, dyad identity, and year. Because individual age, individual rank, and dyadic rank difference all varied across years, I also specified varying slopes for these effects. In addition, I ran a model without any bond strength index because the individual and dyadic variables might already be accounted for in those indices.

Lastly, I ran a series of models that removed maternal brothers from the model to verify that any effects on grooming equality were not being driven by these dyads. The results were unaffected, and therefore I present results only from the previously described models.

(iii) Bond Stability

I ran a series of hierarchical zero-augmented gamma models to examine the stability of male social bonds and whether annual indices were associated with indices from prior years. From one to five years prior, the prior year index was included as an additional fixed effect in the bond strength models (see above). These models examined whether including an index from a previous year explained additional variation, after accounting for all other predictor variables. Naturally, the amount of data available varied by model, either because the prior year index required data from before 1978 (the start of the study), because one or both members of a dyad were not yet adults (≥ 16 years), or because the dyad did not meet the inclusion criteria in a given prior year.

I also ran a series of models that included an interaction between the prior year index and whether dyads had a very strong bond in that prior year; this explored whether dyads with very strong bonds had more stable bonds than dyads with weaker bonds. In four of the 10 models, the model with the interaction was a slightly better fit than its paired model; upon visual inspection of the posterior plots, however, I found no clear evidence of any interaction effect. For clarity and brevity's sake, I therefore do not present results from these additional models.

2.4 Results

Overall, maternal brothers had stronger and more equitable social bonds than other males, whereas the effects of age difference and rank difference were small or nonexistent (Table 2.1). Bonds were also stable for multiple years and endured for up to 13 years.

Table 2.1

Summary of results for bond strength and grooming equality models

	Bond Strength Models		Grooming Equality Models		
	Dyadic Association Index	Dyadic Grooming Index	Model with association index	Model with grooming index	Model with no bond strength index
Maternal kinship	+	+	+	+	+
Age difference	0	0	0	0	0
Rank difference	0	0	–	–	–
Bond strength	n/a		+	+	n/a

$^{+}$ Positive associations between parameter and outcome variable

$^{-}$ Negative associations between parameter and outcome variable

^{0} No (or negligible) association between parameter and outcome variable

2.4.1 *Descriptive Analyses*

Maternal brothers represented 5.9% (N = 1114) and 6.1% (N = 1090) of the unique dyad-years in the association and grooming datasets, respectively. Among dyads with very strong bonds in these two datasets, however, the representation of maternal brothers was 15.7% (N = 25 of 159 strongly-bonded dyads) and 10% (N = 16 of 160), respectively. These data indicate that adult males formed very strong bonds with maternal brothers more often than expected by chance, but that the majority of very strong bonds were formed between other males.

2.4.2 *Sources of Variation in Bond Strength*

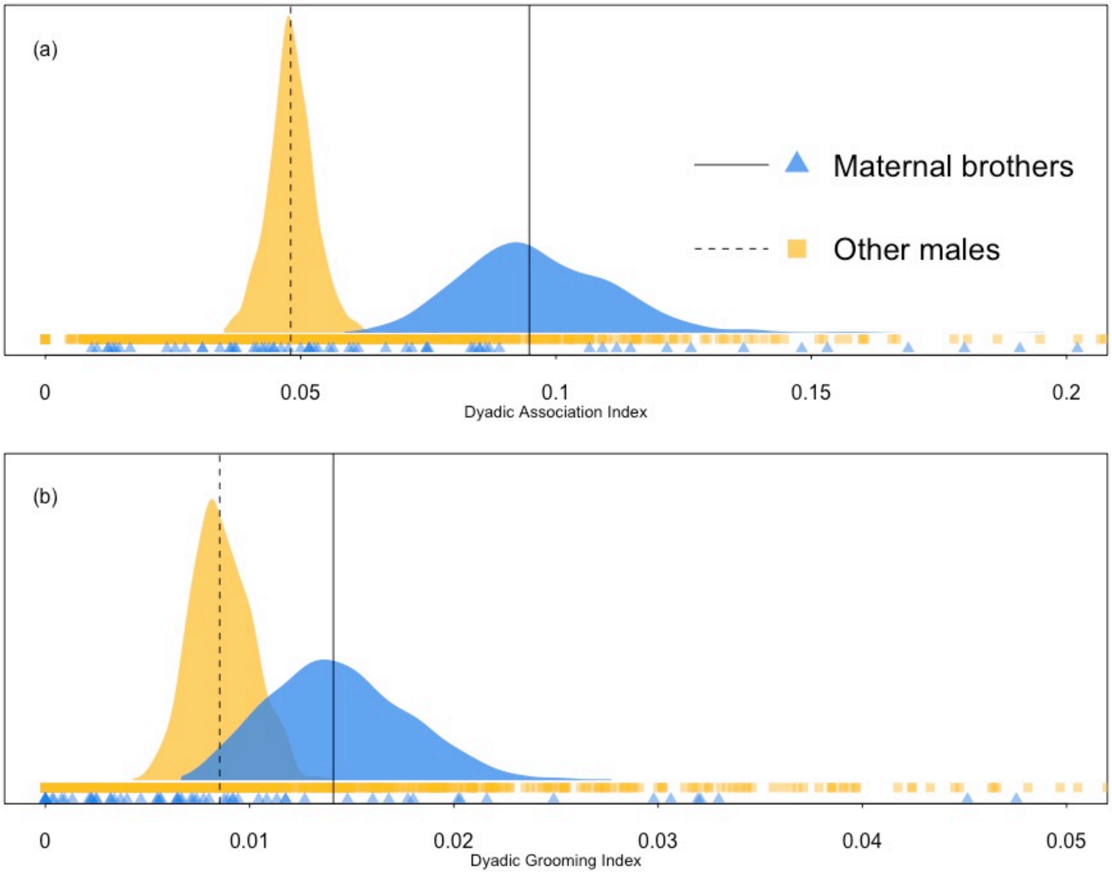
(i) Dyadic Association Index

The association index ranged from 0 to 0.28 (Mean ± SD = 0.05 ± 0.04; *N* = 1114 dyad-years). On average, each male's top two partners were above the mean value of the index across all dyads (top-ranked partner = 0.109 ± 0.049; second-ranked partner = 0.071 ± 0.026; third-ranked partner = 0.057 ± 0.022). Males were each other's strongest (top-ranked) partners in 53% of cases (N = 162 of 304 individual-years).

Maternal brothers had higher posterior median (PM) association indices (PM (89% CI) = 0.095 (0.073, 0.118)) than dyads that were not maternal brothers (0.048 (0.040, 0.055)) (Fig. 2.1a). I report posterior means and standard deviations for all bond strength models in Table 2.2. Although I did not find an overall effect of age difference (Fig. 2.2a) or rank difference (Fig. 2.3a), I found interactions between these variables and maternal kinship. Specifically, maternal brothers who were closer in age had higher association indices than maternal brothers who were farther apart in age, but this age effect did not hold for other dyads (Fig. 2.4a). Similarly, maternal brothers who were closer in rank had higher association indices than maternal brothers that were farther apart in rank, whereas the opposite rank effect was found among other dyads (Fig. 2.5a).

Figure 2.1

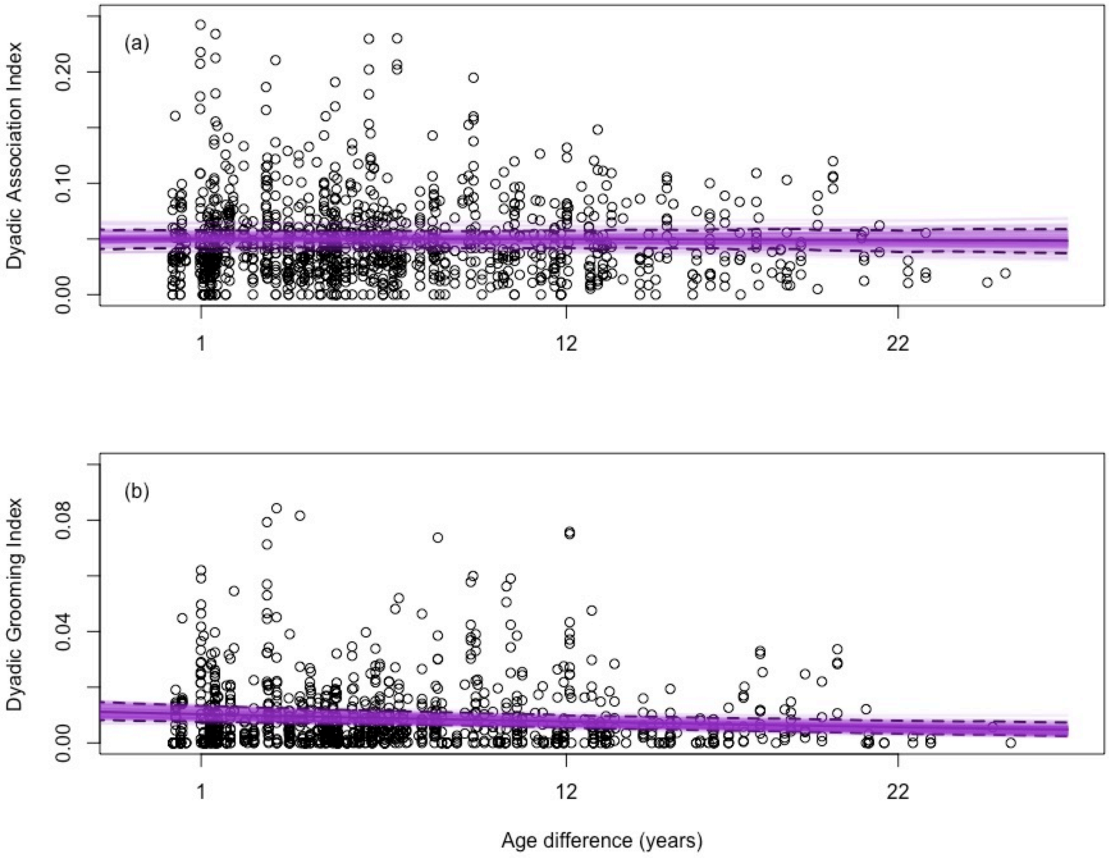
Posterior estimates of bond strength by kinship



Note. Joint posterior estimates of bond strength for maternal brothers (blue) and other males (yellow), as measured by the (a) Dyadic Association Index and (b) Dyadic Grooming Index. Blue triangles and yellow squares are raw data. Vertical solid and dashed lines lie at the posterior median. Certainty in posterior estimates is higher at peaks in the posterior distribution and when posterior confidence intervals are narrower.

Figure 2.2

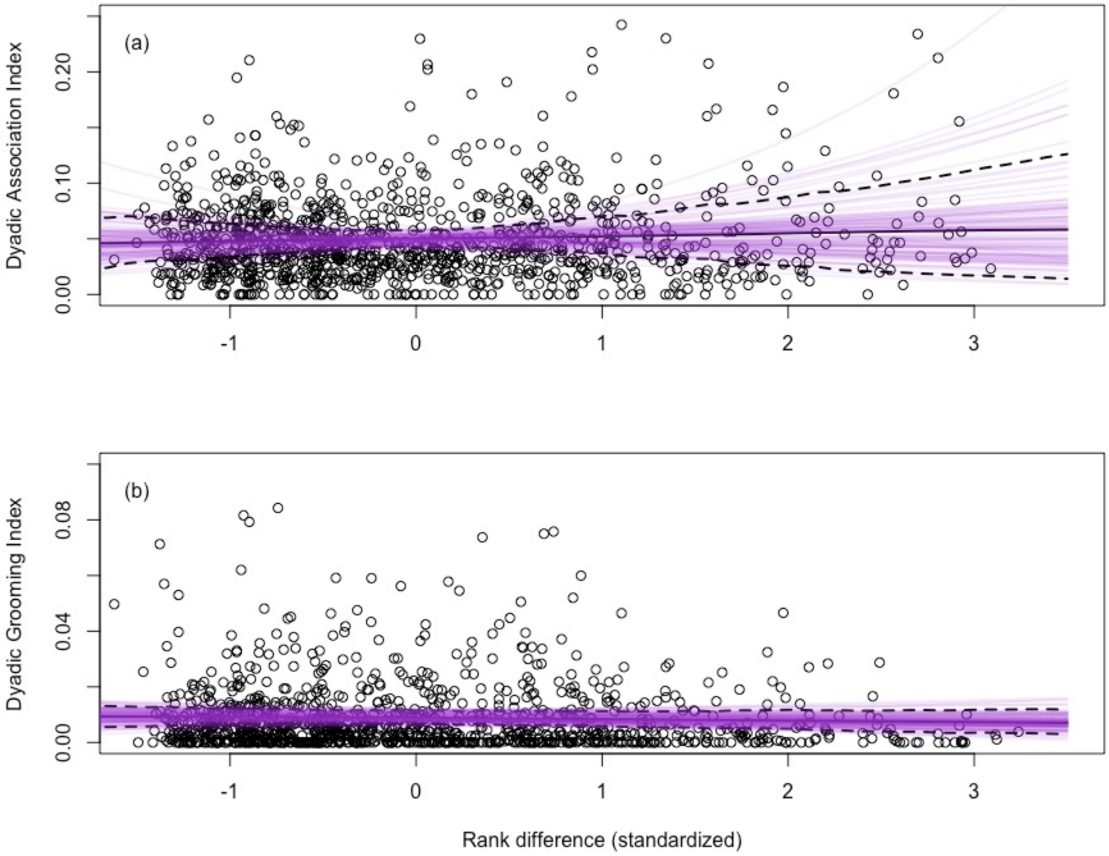
Posterior predictions for the overall influence of age difference



Note. Posterior predictions for the overall influence of age difference on the (a) Dyadic Association Index and (b) Dyadic Grooming Index. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

Figure 2.3

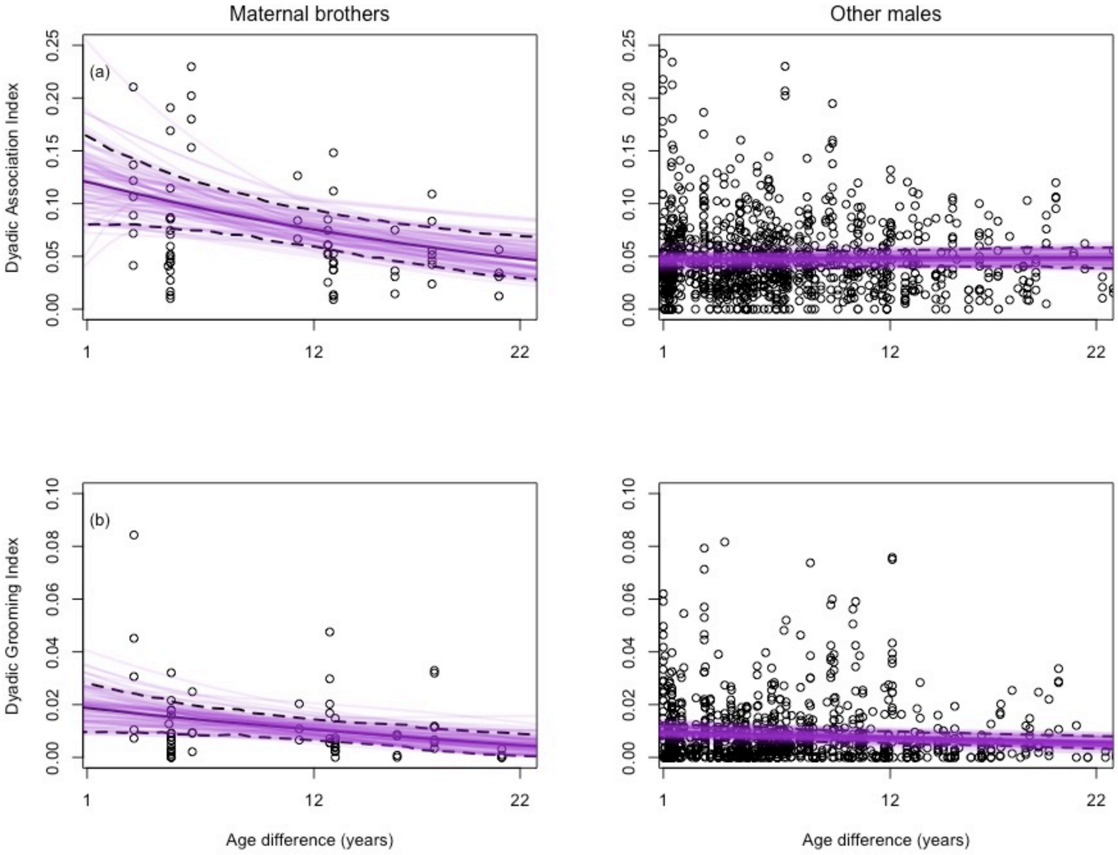
Posterior predictions for the overall influence of rank difference



Note. Posterior predictions for the overall influence of rank difference on the (a) Dyadic Association Index and (b) Dyadic Grooming Index. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions. Because I standardized data on rank difference within years, it is not possible to present values on the x-axis using the real scale; instead, negative values represent dyads similar in rank, zero represents dyads of average rank, and positive values represent dyads of dissimilar rank.

Figure 2.4

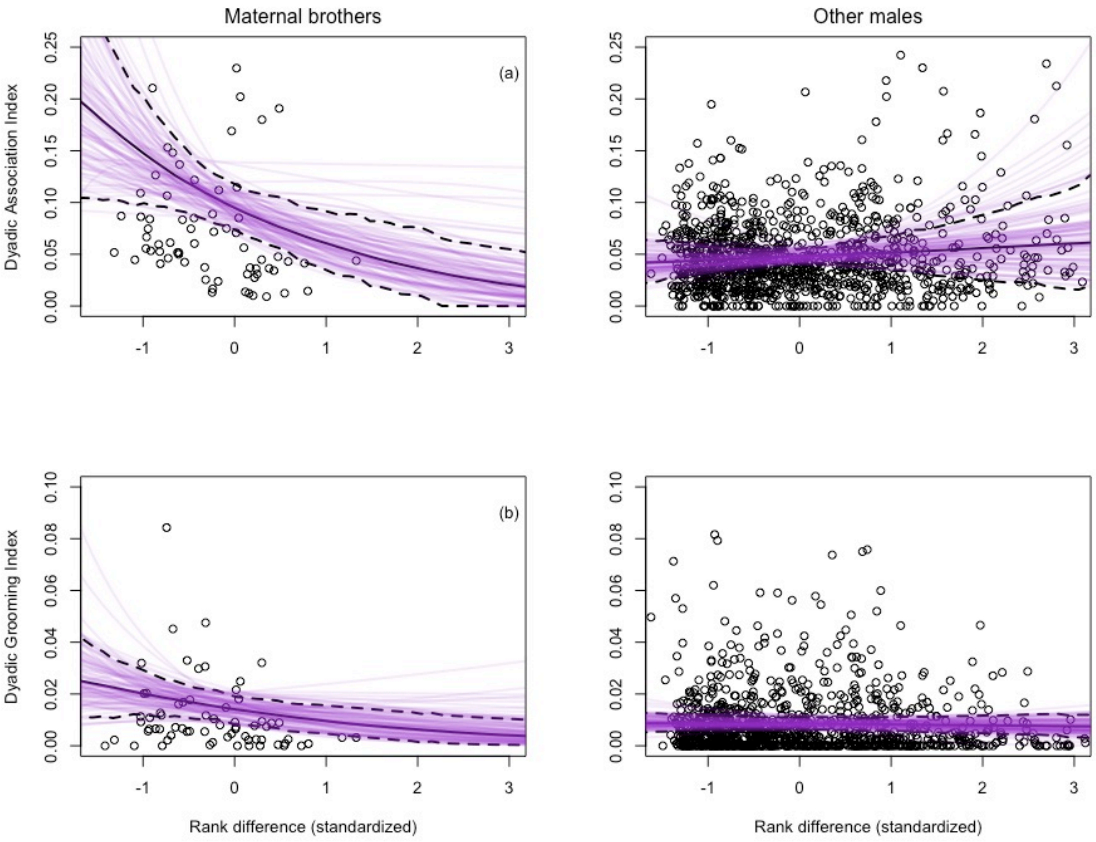
Posterior predictions for the interaction between maternal kinship and age difference



Note. Posterior predictions for the influence of age difference on the (a) Dyadic Association Index and (b) Dyadic Grooming Index. Left-side panels are predictions for maternal brothers; right-side panels are predictions for other males. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

Figure 2.5

Posterior predictions for the interaction between maternal kinship and rank difference



Note. Posterior predictions for the influence of rank difference on the (a) Dyadic Association Index and (b) Dyadic Grooming Index. Left-side panels are predictions for maternal brothers; right-side panels are predictions for other males. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions. Because I standardized data on rank difference within years, it is not possible to present values on the x-axis using the real scale; instead, negative values represent dyads similar in rank, zero represents dyads of average rank similarity, and positive values represent dyads of dissimilar rank

Table 2.2

Parameter estimates for bond strength models

Model	Parameter	Mean	SD
Dyadic Association Index	α_z Intercept	-3.58	0.43
	α_g Intercept	-3.00	0.09
	β_z Rank	-0.10	0.17
	β_g Rank	0.01	0.03
	β_z Age	0.32	0.12
	β_g Age	-0.04	0.03
	β_z Maternal kinship	-2.61	1.32
	β_g Maternal kinship	0.66	0.13
	β_z Rank difference	-0.14	0.20
	β_g Rank difference	0.09	0.03
	β_z Age difference	-0.36	0.20
	β_g Age difference	0.00	0.03
	β_z Maternal brothers * age difference	-0.60	1.33
	β_g Maternal brothers * age difference	-0.23	0.09
	β_z Maternal brothers * rank difference	0.63	1.46
	β_g Maternal brothers * rank difference	-0.51	0.14
	Observations (N)	*1114*	
	Dyads (N)	*157*	
	Individuals (N)	*26*	
Dyadic Grooming Index	α_z Intercept	-1.87	0.47
	α_g Intercept	-4.61	0.14
	β_z Rank	-0.47	0.13
	β_g Rank	0.12	0.04
	β_z Age	-0.12	0.10
	β_g Age	0.11	0.04
	β_z Maternal kinship	-1.70	0.84
	β_g Maternal kinship	0.38	0.20
	β_z Rank difference	-0.25	0.15
	β_g Rank difference	-0.06	0.04
	β_z Age difference	0.19	0.15
	β_g Age difference	-0.10	0.04
	β_z Maternal brothers * age difference	0.74	0.52
	β_g Maternal brothers * age difference	-0.13	0.14
	β_z Maternal brothers * rank difference	-0.31	0.75
	β_g Maternal brothers * rank difference	-0.34	0.19
	Observations (N)	*1090*	
	Dyads (N)	*154*	
	Individuals (N)	*26*	

Note. All parameters with a subscript of z correspond with the Bernoulli component of the model, while those with a subscript of g correspond with the gamma component. Negative coefficients in the Bernoulli component indicate a lower probability of observing a DSI of zero, while positive values in the gamma component indicate parameters that are associated with higher DSI values and stronger bonds

(ii) Dyadic Grooming Index

The grooming index ranged from 0 to 0.16 (Mean ± SD = 0.009 ± 0.014; N = 1090 dyad-years). On average, each male's top two partners were above the mean value of the index (top-ranked partner = 0.027 ± 0.022; second-ranked partner = 0.016 ± 0.014; third-ranked partner = 0.011 ± 0.010). Males were each other's strongest (top-ranked) partners in 42% of cases (N = 124 of 302 individual-years); on average, males spent 39.5% (SD = 0.21) of their total grooming time grooming with their top grooming partner.

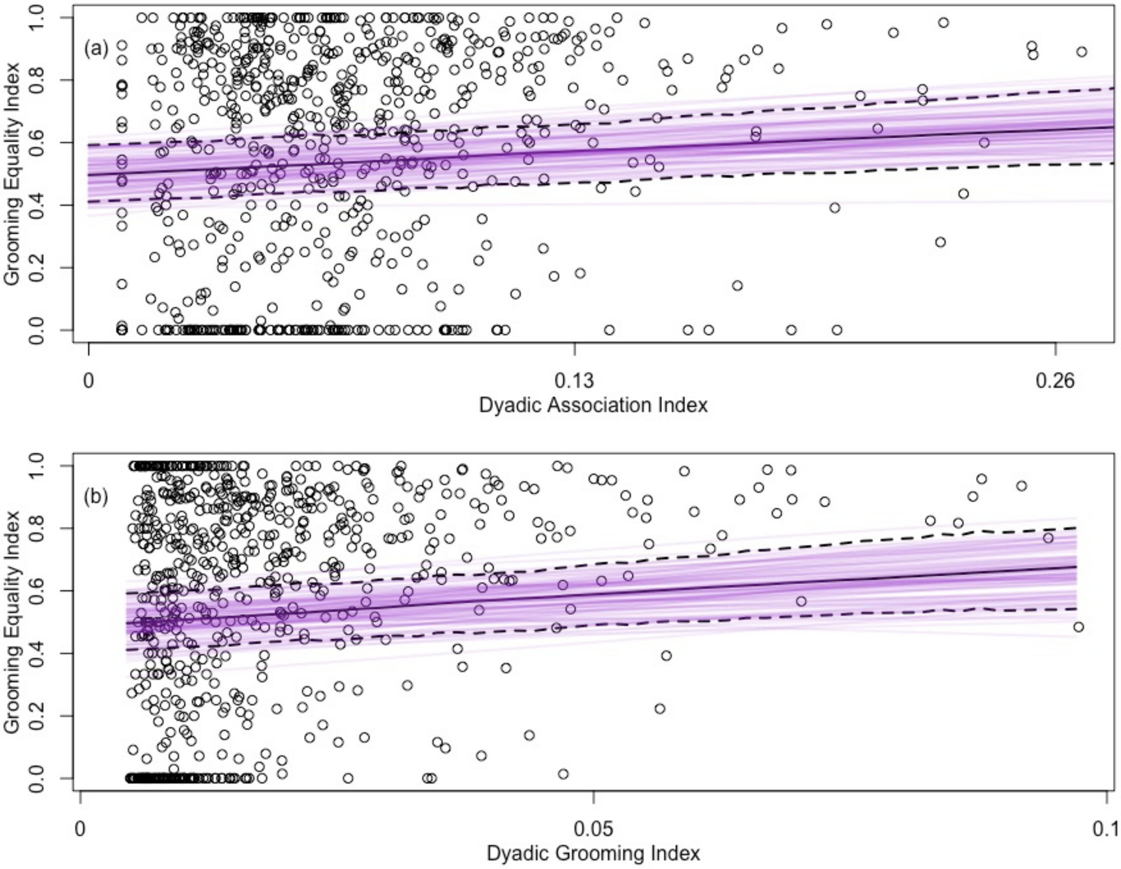
Maternal brothers had higher posterior median (PM) grooming indices (PM (89% CI) = 0.014 (0.008, 0.019)) than other dyads (0.008 (0.006, 0.011)) (Fig. 2.1b). Neither age difference (Fig. 2.2b) nor rank difference (Fig. 2.3b) had an overall effect on grooming indices, but I again found interactions between these variables and maternal kinship. Maternal brothers who were closer in age had slightly elevated grooming indices compared to maternal brothers who were farther apart in age (Fig. 2.4b). Similarly, maternal brothers who were closer in rank had higher grooming indices than maternal brothers that were farther apart in rank (Fig. 2.5b).

2.4.3 *Sources of Variation in Grooming Equality*

The median Grooming Equality Index was 0.68 (Mean ± SD = 0.58 ± 0.34; N = 702 dyad-years). Both bond strength indices were positively associated with annual grooming equality indices (Fig. 2.6). I report posterior means and standard deviations for all grooming equality models in Table 2.3. I also found that dyads that were closer in rank groomed more equitably than dyads that were farther apart in rank (Fig. 2.7), but annual grooming equality indices were not associated with age similarity. Lastly, although maternal brothers groomed more equitably than other dyads, the estimates around this effect were highly variable. Given that maternal brothers formed stronger bonds than other dyads, however, this effect could have been masked by the bond strength predictor. I therefore ran one additional model without any bond strength predictor. In this model, there was a stronger positive association between maternal kinship and grooming equality, although their posteriors continued to overlap (Fig. 2.8).

Figure 2.6

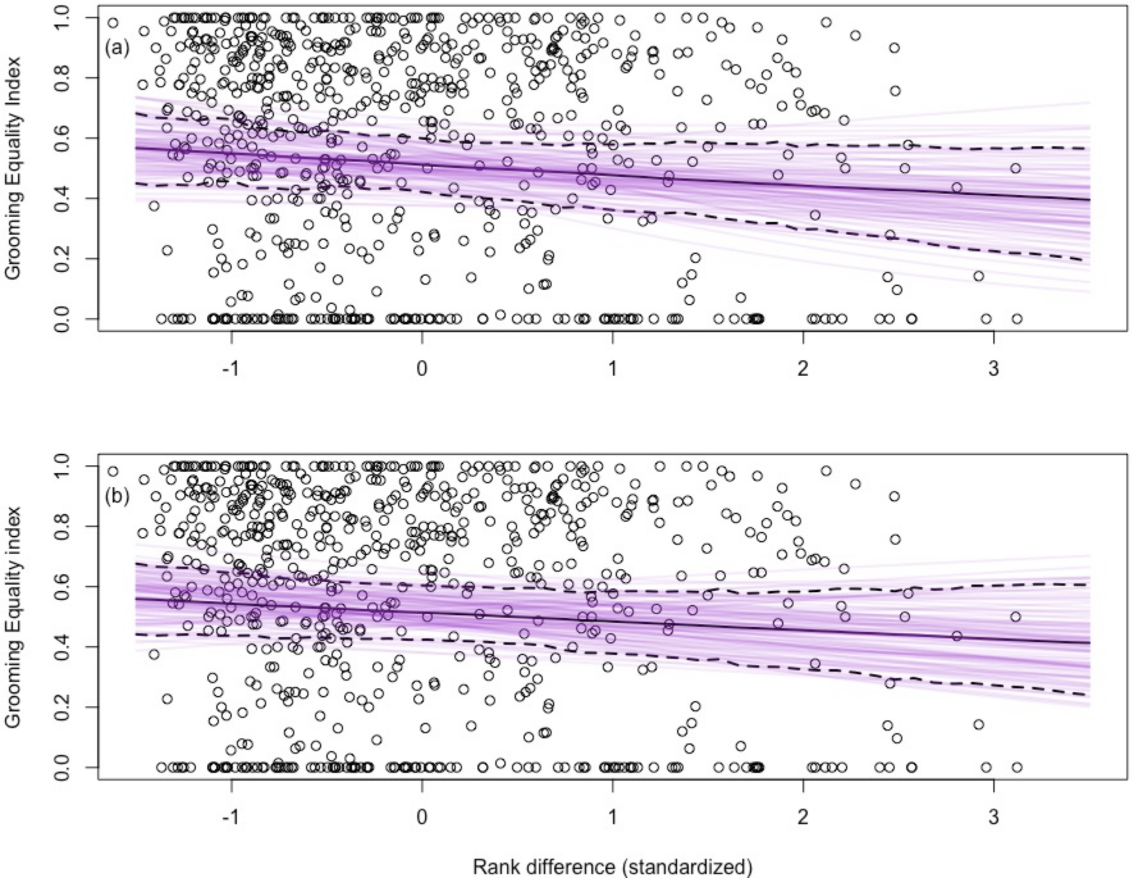
Posterior predictions for the influence of bond strength on grooming equality



Note. Posterior predictions for the influence of bond strength on the Grooming Equality Index, as measured by the (a) Dyadic Association Index and (b) Dyadic Grooming Index. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

Figure 2.7

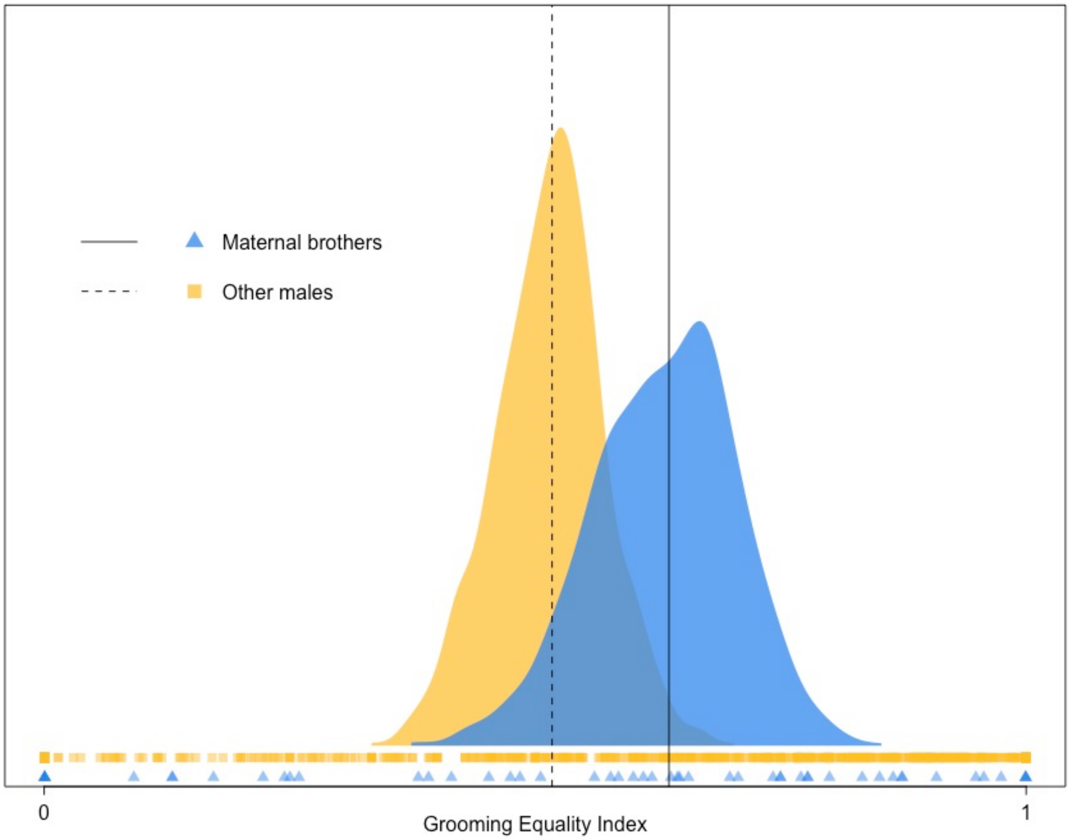
Posterior predictions for the influence of rank difference on grooming equality



Note. Posterior predictions for the influence of rank difference on the Grooming Equality Index, after controlling for the (a) Dyadic Association Index and (b) Dyadic Grooming Index. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

Figure 2.8

Posterior estimates of grooming equality by kinship



Note. Posterior estimates of grooming equality for maternal brothers (blue) and other males (yellow). Blue triangles and yellow squares are raw data. Vertical solid and dashed lines lie at the posterior median. Certainty in posterior estimates is higher at peaks in the posterior distribution and when posterior confidence intervals are narrower.

Table 2.3

Parameter estimates for grooming equality models

Model	Parameter	Mean	SD
Model with association index	α Intercept	-0.05	0.18
	β Rank	0.14	0.06
	β Age	0.04	0.05
	β Rank difference	-0.14	0.07
	β Age difference	-0.07	0.07
	β Maternal kinship	0.33	0.26
	β Dyadic association index	0.13	0.05
	β Male community size	0.00	0.10
Model with grooming index	α Intercept	-0.08	0.18
	β Rank	0.14	0.07
	β Age	0.02	0.05
	β Rank difference	-0.11	0.07
	β Age difference	-0.05	0.07
	β Maternal kinship	0.45	0.26
	β Dyadic grooming index	0.13	0.06
	β Male community size	-0.03	0.10
Model with no bond strength index	α Intercept	-0.03	0.18
	β Rank	0.15	0.07
	β Age	0.04	0.05
	β Rank difference	-0.12	0.07
	β Age difference	-0.07	0.07
	β Maternal kinship	0.48	0.26
	β Male community size	-0.04	0.10
	Observations (N)	*702*	
	Dyads (N)	*126*	
	Individuals (N)	*26*	

Note. The response variable was each dyad's annual grooming equality index. Positive posterior means indicate parameters that are associated with more equitable grooming relationships.

2.4.4 *Stability of Social Bonds*

I first examined whether each adult male's strongest relationships were more stable than his weakest relationships. Across both bond strength indices, a male's strongest relationship was somewhat more stable than his weakest relationship, but his strongest two relationships were not more stable than his weakest two relationships (Table 2.4).

Table 2.4

Mean stability of each male's strongest bonds compared to his weakest bonds

	Mean PSI of Strongest Relationship(s)		*Mean PSI of Weakest Relationship(s)*	
	Mean	*SD*	*Mean*	*SD*
Dyadic Association Index (one partner)	0.56	0.21	0.41	0.25
Dyadic Association Index (two partners)	0.67	0.1	0.64	0.15
Dyadic Grooming Index (one partner)	0.59	0.21	0.33	0.18
Dyadic Grooming Index (two partners)	0.73	0.07	0.66	0.09

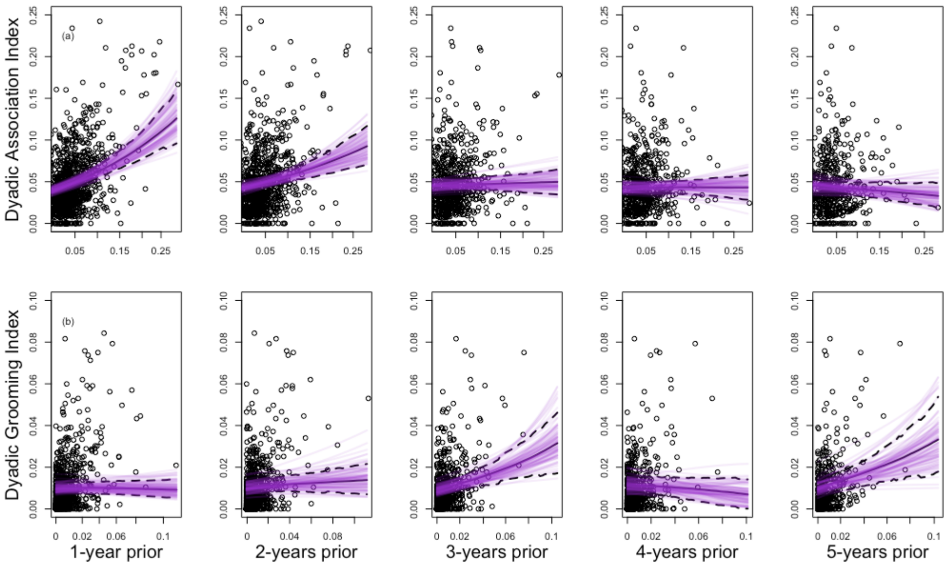
Note. Bond stability indices are based on the Partner Stability Index. Values of 0 indicate unstable partnerships on an individual level, while values of 1 indicate completely stable partnerships. I calculated four indices for each index: (1) stability of a male's strongest bond partner, (2) stability of a male's weakest bond partner, (3) stability of a male's strongest two bond partners, and (4) stability of a male's weakest two bond partners

(i) Dyadic Association Index

Association indices from one and two years prior to a given year explained additional variation not captured by other predictor variables (Fig. 2.9a). I report posterior means and standard deviations for all bond stability models in Table S2.1 (Appendix A). From three to five years prior, however, association indices did not positively predict indices of future years.

Figure 2.9

Posterior predictions for the influence of prior-year bond strength indices on present-year bond strength indices



Note. Posterior predictions for the influence of prior-year bond strength indices on present-year bond strength indices, as measured by the (a) Dyadic Association Index and (b) Dyadic Grooming Index. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

(ii) Dyadic Grooming Index

Grooming indices from prior years had highly variable and inconsistent associations with future year indices. The prior year grooming indices did not consistently explain additional variation after accounting for other variables (Fig. 2.9b).

2.4.5 *Bond Duration*

Although bonds were stable at the community level for multiple years, there was substantial variation among dyads. Specifically, the maximum number of consecutive years that dyads formed a very strong bond, allowing for one-year gaps, ranged from 0 to 9 years based on the association index (Mean ± SD = 0.96 ± 1.57; *N* = 157) and 0 to 13 years (Mean ± SD = 0.97 ± 1.83; *N* = 154) based on the grooming index.

2.5 Discussion

2.5.1 *Variation in bond strength and quality*

Adult male chimpanzees in the Kasekela community at Gombe National Park, Tanzania, formed strong and equitable social bonds. Not only were these bonds stable across the community for multiple years, but several bonds endured for 7 to 13 years. Maternal brothers formed stronger bonds than other dyads, and maternal brothers who were close in age or close in rank formed the strongest bonds. Among other dyads that were not maternal brothers, the strength of social bonds was not associated with either age difference or rank difference. In addition, adult male dyads with stronger bonds had higher quality bonds. Specifically, they groomed more equitably than dyads with weaker bonds, as did maternal brothers and dyads close in rank. Although kin selection theory allows for relaxed reciprocation of altruistic behavior among close kin, this was not the case. The finding that maternal brothers groomed more equitably than other dyads is consistent with prior studies (Mitani, 2009a). The other findings are also consistent with previous studies from other chimpanzee communities, adding additional support to the view that adult male social bonds are a chimpanzee universal (Kanyawara: Gilby & Wrangham, 2008; Ngogo: Langergraber et al., 2007; Mitani, 2009a, Watts, 2000a).

Although adult male chimpanzees form strong, stable bonds, and groom more equitably with strong bond partners, there is no clear explanation as to what determines adult male partner choice. Kinship, the best predictor of bond strength, explains only a limited number of strongly bonded dyads in this study. These dyads, which require the birth of two males that both survive to adulthood, are uncommon, representing only 6% of dyads in this study and 1.5% of dyads at Ngogo (Langergraber et al., 2007; Mitani, 2009a). Even more uncommon are maternal brothers who are close in age; in this study, these dyads formed the strongest bonds but require the birth of two consecutive males that each survive to adulthood. These results are consistent with previous work at Ngogo, where maternal brothers formed strong bonds but most strong social bonds were nonetheless formed by unrelated or distantly related males (Langergraber et al., 2007). In addition, age similarity and rank similarity accounted for some of the variation in coalition formation, meat sharing, and patrol behavior at Ngogo but did not predict association, grooming, or proximity (Mitani, Watts, Pepper, et al., 2002), and these effects of age and rank difference were small or nonexistent in this study, particularly among non-kin.

Together, these studies suggest that relationship strength in male chimpanzees is more than a simple accounting of basic characteristics such as kinship, age, and rank. In addition to these factors, dyads may possess some distinct quality that engenders strength and stability, such as compatible personalities. To date, personality homophily (forming social bonds with individuals of similar personality) has received relatively little attention. In humans, studies have found mixed results (Ilmarinen et al., 2016, 2017; Lee et al., 2009; Montoya et al., 2008; Selfhout et al., 2010). Among non-human animals, studies in captive chimpanzees (Massen & Koski, 2014) and Assamese macaques (*Macaca assamensis*) (Ebenau et al., 2019) have found that the strength of social bonds are associated with similarity in personality traits. In baboons (*P. ursinus*) (Seyfarth et al., 2014), however, personality homophily explains social bonds among maternal sisters but not non-kin. There is currently minimal data on personality in wild chimpanzees (but see Weiss et al., 2017 for a descriptive dataset on personality among chimpanzees at Gombe National Park). In light of multiple studies emphasizing the lack of homophily in kinship, age and rank in the friendships of male chimpanzees, personality homophily deserves greater attention.

Overall, my results contrast with those in several other species (Seyfarth & Cheney, 2012), including baboons (*P. cynocephalus* and *P. ursinus*), where stronger and more equitable bonds are formed not only by female kin but also among females that are close in age and rank (Silk et al., 2010a; Silk, Altmann, et al., 2006). Because of high paternity skew in these species, age similarity is a useful proxy for paternal relatedness (Alberts, 1999; Altmann, 1979; Smith et al., 2003; Widdig et al., 2001). Chimpanzees, however, typically have low paternity skew (Langergraber et al., 2007; Surbeck, Langergraber, et al., 2017), which may explain why unrelated males that are close in age do not form strong bonds. I also found differences compared to other species in the stability of different partner ranks. Although I found some evidence that male chimpanzees had more stable relationships with their strongest partners than their weakest partners, the effects were not as pronounced as in yellow baboons (*P. cynocephalus*) (Silk et al., 2012). In yellow baboons, the dramatic effects of kinship could mean all relationships aside from kin are essentially random. By contrast, male chimpanzees may have greater preferences and aversions for all males in the community, which would make weak relationships more stable than in baboons.

2.5.2 *Methodology*

Researchers use a variety of methods to study animal social relationships (Silk et al., 2013; Whitehead, 2008). This study, which used two measures of bond strength, reveals important biological insights. Based on these results, party-level association appears to be a better measure of male chimpanzee social preferences than grooming, at least in the Kasekela community. First, maternal brothers were more distinct from other dyads in their associations than in their grooming. Second, association was a stronger predictor of grooming equality than was grooming. Third, association was more stable on a year-to-year basis than grooming. What might explain this? Although I and others have used grooming as a measure of bond strength, it also functions to remove parasites (Barton, 1985; Hutchins & Barash, 1976; Mooring et al., 2004; Tanaka & Takefushi, 1993) and as a mode of exchange (Borgeaud & Bshary, 2015; Kaburu & Newton-Fisher, 2015; Noë & Hammerstein, 1994; Schino, 2001; Tiddi et al., 2011). This could add noise to attempts to measure bond strength with grooming, as only some proportion of male-male grooming has a purely social function (Dunbar, 1991). By contrast, the association index, which is based on party composition in small groups, may be a better proxy of social preference (see also Newton-Fisher, 1999).

This study also provides important insights into the effect of methodological decisions. Despite differences in the methods used, the patterns I found in adult male social bonds are overall quite similar to prior studies (Gilby & Wrangham, 2008; Langergraber et al., 2007; Mitani, 2009a), suggesting that methodological variation may not be of primary importance. Of course, there is obvious value in using identical methods wherever possible, which presents a tradeoff. On the one hand, internal consistency within studies facilitates longitudinal analyses. On the other hand, converging on a unified set of methods would provide opportunities for more accurate comparisons between study populations. Going forward, it would be beneficial for researchers to incorporate a suite of standardized behaviors into data collection protocols to make studies more comparable, without jeopardizing compatibility with data collected in previous years.

2.5.3 *Conclusion*

Kinship is a widespread driver of cooperation among animals (Smith, 2014), but male chimpanzees present an intriguing case, similar to humans, where strong social bonds and high levels of cooperation exist despite the limited impact of kinship. Similarity in age or rank also do not adequately explain male partner choice. Male chimpanzees are unusual in that social intelligence and cooperation can be exceptionally helpful in climbing the dominance hierarchy (Goodall, 1986; Mitani, 2009b) but typical, dependable partners such as close kin are uncommon. Male chimpanzees may therefore resort to identifying compatible partners through other means. Further studies in chimpanzees and other species are needed to better understand the socioecological factors driving these patterns.

2.6 References

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CHAPTER 3

SOCIAL BONDS PREDICT DOMINANCE TRAJECTORIES IN ADULT MALE CHIMPANZEES

3.1 Abstract

In some species, individuals form well-differentiated and affiliative social relationships that facilitate cooperation and confer adaptive benefits, but few studies of males have linked same-sex social bonds to increased fitness. Among mammals, adult male chimpanzees form some of the strongest and most stable social bonds, and several studies have found that higher ranking males achieve greater reproductive success. No study in chimpanzees, however, has demonstrated a link between social bonds and dominance trajectories. To fill this gap, I used 37 years of data from Gombe National Park, Tanzania, to test the hypothesis that social bonds in adult male chimpanzees predict changes in dominance strength, which were measured by annual changes in mean Elo scores. Across 24 adult males, I found that social bonds, which were identified using both association in small groups and grooming activity, showed positive relationships with changes in dominance strength. From previous studies, the most likely mechanism for the observed relationship between adult male bond strength and dominance trajectories is the formation of cooperative coalitions, by which males with stronger bonds leverage established relationships to maintain or increase their position in the dominance hierarchy. Given the fission-fusion social structure of chimpanzees, both party-level associations and grooming relationships are essential components of male social bonding, and these results, in combination with prior studies, suggest that having strong social

bonds is a valuable strategy for achieving higher rank and, ultimately, increased reproductive success.

3.2 Introduction

Understanding the evolution of cooperation is a central goal in animal behavior research (Dugatkin, 2002; Silk, 2005). In several species, individuals form well-differentiated and affiliative social relationships, also known as social bonds, which foster cooperation and are linked to fitness benefits (reviewed in: Ostner & Schulke, 2018; Seyfarth & Cheney, 2012; Silk, 2007). For example, in humans, strong social ties bestow fitness benefits such as improved health and greater longevity (Holt-Lunstad et al. 2010; Shor & Roelfs, 2015; reviewed in: Holt-Lunstad, 2018). Similarly, strong social bonds are associated with greater longevity in female yellow and chacma baboons (*Papio cynocephalus* and *P. ursinus*) (Archie et al., 2014; Silk et al., 2010b) and reduced infant mortality in yellow and chacma baboons (Cheney et al., 2016; Silk et al., 2003, 2009), bottlenose dolphins (*Tursiops* sp.) (Frère et al., 2010; Stanton & Mann, 2012), and feral horses (*Equus caballus*) (Cameron et al., 2009). Among males, few studies have addressed the adaptive value of social bonds, but bonds are believed to help individuals compete for dominance rank and mating access (reviewed in: Ostner & Schülke, 2014). To date, the clearest evidence of this is found in male Assamese macaques (*Macaca assamensis*), in which males with stronger social bonds exhibit greater increases in rank and have higher paternity success (Schülke et al., 2010).

Chimpanzees are an excellent species in which to investigate the benefits of male-male social bonds. They live in large multi-male, multi-female communities that associate in subgroups, or parties, that change in size and composition throughout the day (Boesch & Boesch-Achermann, 2000; Goodall, 1986). Adult male chimpanzees are highly gregarious (Arnold & Whiten, 2003; Boesch & Boesch-Achermann, 2000; Gomes et al., 2009; Goodall, 1986; Newton-Fisher & Lee, 2011; Pepper et al., 1999; Watts, 2000a, 2000b), express clear and consistent preferences in association partners (Bray & Gilby, 2020; Gilby & Wrangham, 2008; Newton-Fisher, 1999), and form some of the strongest and most enduring bonds among mammals (Bray & Gilby, 2020; Gilby & Wrangham, 2008; Langergraber et al., 2007; Mitani, 2006, 2009a, 2009b; Mitani, Watts, Pepper, et al., 2002; Watts, 2002). Male chimpanzees also preferentially form strong and equitable bonds with close kin (Bray & Gilby, 2020; Langergraber et al., 2007; Mitani, 2009a), reconcile more frequently with strong bond partners (Preis et al., 2018), and are more likely to intervene when a strong bond partner is grooming with another individual (Mielke et al., 2017), all of which suggest that strong bonds have important fitness consequences. Furthermore, affiliative social interactions, which contribute to the formation and maintenance of bonds, are linked to the frequency of coalitions (Mitani, 2006; Watts, 2002), a behavior in which at least two individuals direct aggression toward others in a coordinated manner (Bissonnette et al., 2014). Coalitions, in turn, are linked to the acquisition of high rank (Gilby et al., 2013; Goodall, 1986; Mitani, 2009b; Muller & Mitani, 2005), which is associated with greater reproductive success (Boesch et al., 2006; Feldblum et al., under review; Inoue et al., 2008; Langergraber et al., 2013; Newton-Fisher et al., 2010; Wroblewski et al., 2009). No study, however, has demonstrated a relationship between the strength of social bonds and dominance trajectories in male chimpanzees.

This study aims to fill a gap in our understanding of how social bonds relate to fitness in male chimpanzees. Using 37 years of data on adult male chimpanzees at Gombe National Park, Tanzania, I test the hypothesis that same-sex social bonds predict changes in dominance strength. Previous studies at Gombe have documented well-differentiated social relationships among males (Bray & Gilby, 2020), identified correlations between position in a coalitionary network and both paternity success and rank change (Gilby et al., 2013), and found that high rank (Wroblewski et al., 2009) and alpha status (Feldblum et al., under review) correlate with paternity success. Here, I assess whether patterns of association and grooming, two behaviors involved in social bond formation and maintenance, predict changes in dominance strength.

3.3 Methods

3.3.1 *Study Site, Subjects, and Data Collection*

I studied the Kasekela chimpanzee (*P. t. schweinfurthii*) community in Gombe National Park, Tanzania, which encompasses approximately 35 km^2 of riverine forest, woodland, and grassland (Clutton-Brock & Gillett, 1979). Observations of the Kasekela community began in 1960, and chimpanzees were fully habituated by 1966 through the use of banana provisioning at a feeding station (Goodall, 1986; Wilson, 2012). Feeding continued at low levels until 2000 (Wilson, 2012). Since 1973, Tanzanian field assistants have conducted full-day focal observations (Altmann, 1974) of chimpanzees in this community (Wilson, 2012). As described elsewhere (Wilson, 2012), teams of two observers follow all chimpanzees that travel independently of their mothers approximately once per month. During these focal follows, one observer records party composition, including when individuals join and leave the focal chimpanzee's party. Two individuals are considered to have 'arrived' together if they either (i) are present in the party at the start of a focal follow or (ii) join a party within five minutes of each other (Williams et al., 2002). A second observer records a continuous narrative of the behavior of the focal chimpanzee and conspicuous non-focal activities such as submissive pant-grunt vocalizations. A relational database, including both behavioral and demographic data, is maintained by the Gombe Research Consortium and coordinated by the Institute of Human Origins at Arizona State University.

3.3.2 *Analyses*

I analyzed behavioral data from 1979 to 2015, including males in annual analyses if they were ≥ 16 years old (Bray & Gilby, 2020; Goodall, 1986; Mitani, 2009a; Sandel et al., 2016). This age generally corresponds to physical (full body size) and social maturity (entry into the adult male dominance hierarchy). In total, I examined annual changes in dominance strength for 24 males. I excluded one male, Pax, from all analyses because he sustained severe testicular injuries before adulthood and consequently never integrated into the adult male dominance hierarchy (Goodall, 1986).

The birthdates of 18 males born in the Kasekela community after the study began were estimated based on both their size and appearance when first observed as well as the dates of previous sightings of the mother without an infant (Hill et al., 2001; Strier et al., 2010). The median difference between the minimum and maximum birthdates was 7 days (Mean ± SD = 8.4 ± 9.5, N = 18). For the six remaining males, the birthdates were estimated based on morphological characteristics and familial relationships; the median difference between the minimum and maximum birthdates was 548 days (Mean ± SD = 669 ± 427 days, N = 6).

(i) Dominance Strength

To estimate changes in dominance strength, I first identified all pant-grunt vocalizations (formal and unambiguous signals of submission in chimpanzees: Bygott, 1979; Goodall, 1986) between males that were ≥ 12 years old. I included pant-grunts with clear actors and recipients, which included interactions when two or more chimpanzees pant-grunted to one individual but excluded cases in which a single chimpanzee pant-grunted to multiple individuals. These interactions were used to calculate Elo scores, which estimate a subject's dominance strength while accounting for demographic changes and missing data (Albers & de Vries, 2001; Neumann et al., 2011). Elo scores are also highly correlated with traditional indices that aggregate over longer periods (e.g. I&SI and David's scores, Neumann et al., 2011). To calculate daily Elo scores, I used a maximum-likelihood implementation of the Elo method using the 'EloOptimized' package (Feldblum et al., 2019; Foerster et al., 2015) in R v.3.6.2 (R Core Team, 2019). To provide a burn-in period, I restricted my analyses to data from 1979 onward because pant-grunts were recorded consistently beginning in 1978. Additionally, by including males that were ≥ 12 years old in my Elo score calculations, I ensured that all pant-grunts relevant to the hierarchy were incorporated into estimates of dominance strength (e.g., adult males pant-grunting to adolescent males) and that individuals had accurate Elo scores by the time they entered adulthood.

I analyzed changes in Elo scores on an annual basis, balancing a desire to capture meaningful changes in dominance strength with the need for sufficiently long periods to accumulate accurate estimates of bond strength. To do so, I estimated annual dominance strength for each male by calculating a mean of daily Elo scores (Bray & Gilby, 2020), which provided an estimate of a male's dominance strength over each annual period. I considered identifying changes in dominance strength across stable and unstable periods, but Elo scores change continuously, and reversals in ordinal rank occur often enough to preclude a straightforward delineation of stable and unstable periods (Figs. 3.6-3.9; Appendix B).

(ii) Sociality Indices

Previous studies have investigated the benefits of sociality using two general approaches. One approach measures each individual's sociality across one or more affiliative social behaviors (Ellis et al., 2019; Silk et al., 2003), without assessing how social interactions are distributed across social partners. An alternative approach estimates the overall strength of each individual's dyadic social relationships (Ellis et al., 2019; Schülke et al., 2010). Because no consensus exists on the most biologically meaningful method (Ellis et al., 2019; Ostner & Schulke, 2018; Silk et al., 2013), and different indices may assess different aspects of male-male social integration or connectedness, I calculated a variety of sociality indices that estimated either general gregariousness (approach 1) or were based on measures of dyadic bond strength (approach 2). I calculated all indices using either party-level association or grooming data (see below), which are standard metrics for assessing adult male social bonds in chimpanzees (Bray & Gilby, 2020; Gilby & Wrangham, 2008; Goodall, 1986; Mitani, 2009b; Newton-Fisher, 1999; Samuni et al., 2018; Watts, 2000a, 2002). All indices within each category were positively correlated to varying degrees (Figures S3.1 and S3.2; Appendix B), and I used model comparisons to evaluate a total of 24 models that each included one sociality index (Table 3.1).

Table 3.1

Summary of male sociality indices and overall results from statistical models

Category	Sociality Index	Association Models	Grooming Models	
Indices based on dyadic bond strength	(A1, G1, G7) Sum of all dyadic indices	+	0	+
	(A2, G2, G8) Mean of all dyadic indices	+	0	+
	(A3, G3, G9) Sum of dyadic indices that are above the mean^	+	0	+
	(A4, G4, G10) Sum of dyadic indices that are ≥ 1 SD above the mean^	+	0	+
	(A5, G5, G11) Number of dyadic indices that are above the mean^	+	0	+
	(A6, G6, G12) Number of dyadic indices that are ≥ 1 SD above the mean^	+	0	0
Indices based on general gregariousness	(A7) Proportion of arrivals with adult males	+	n/a	
	(A8) Mean number of adult males in each arrival	+	n/a	
	(G13) Proportion of time grooming with adult males (total)	n/a	+	
	(G14) Proportion of time grooming with adult males (mutual)	n/a	+	
	(G15) Proportion of time grooming with adult males (give)	n/a	+	
	(G16) Proportion of time grooming with adult males (receive)	n/a	+	

Note. A1-A8 refer to indices based on party-level association; G1-G16 refer to indices based on grooming activity (G1-G6 control for time together; G7-G12 control for observation time)

$^{\wedge}$ Indices based on the 'mean' value refer to the mean of the index across all dyads in a given year

$^{+}$ Positive associations between the parameter and annual change in mean Elo score

^{0} No (or negligible) overall association between the parameter and annual change in mean Elo score

For indices based on party-level associations, I calculated two annual measures of general gregariousness. First, I calculated the proportion of each male's first arrivals in a day that occurred in association with ≥ 1 other adult male, a measure that was positively correlated with the proportion of time spent in parties with adult males ($r = 0.92$; $p < 0.0001$; $N = 328$). Second, I calculated the mean adult male party size across each male's first arrivals. I also calculated four annual indices of general gregariousness based on grooming activity: (1) the proportion of focal time spent grooming adult males (mutual, give, or receive), (2) the proportion of focal time spent mutually grooming adult males, (3) the proportion of focal time giving grooming to other adult males, and (4) the proportion of focal time receiving grooming from other adult males. Mutual grooming bouts are those in which both partners simultaneously groom each other (e.g. Machanda et al., 2014).

To generate individual sociality indices based on the strength of each male's dyadic associations, I calculated a dyadic association index as follows:

$$\frac{J_{i,j}}{A_i + A_j - J_{i,j}}$$

where $J_{i,j}$ is the number of joint arrivals for each dyad, A_i is the total number of arrivals of male i, and A_j is the total number of arrivals of male j (Figure S3.3; Appendix B) (Cairns & Schwager, 1987). This index estimates how often pairs of adult males were together in parties (Bray & Gilby, 2020; Foerster et al., 2015; Williams et al., 2002) and was positively correlated with indices based on the proportion of time spent together ($r = 0.78$; $p < 0.0001$; $N = 2668$). To avoid non-independent arrivals from individuals leaving and re-joining a party throughout the day, I included only the first (earliest) arrival of an individual per day. I further restricted the data to include only arrivals of four adult individuals or fewer (to be included, females had to be ≥ 15 years old, the mean age at first birth at Gombe: Walker et al. 2018), because associations of large numbers of individuals are more likely to reflect grouping for reasons other than social preference, such as a high-quality food resource or a female in estrous (Matsumoto-Oda et al., 1998; Mitani, Watts, & Lwanga, 2002). Using these dyadic indices, I calculated six annual sociality measures for each male (Table 3.1). Measures included the sum of all dyadic indices, the mean of all dyadic indices, and the number of dyadic indices above multiple thresholds. Note that dyadic indices based on arrivals in small groups do not measure general gregariousness but rather estimate the strength of male-male partner preferences; correlations between sociality indices based on dyadic indices and the mean number of adult males in each arrival were weak (Figure S3.1; Appendix B). Lastly, if either member of a dyad had fewer than 21 arrivals in parties of four or fewer in a year (Bray & Gilby, 2020; Foerster et al., 2015), I excluded their indices from the association analyses. This criterion ensured that data would not be biased by poor sampling, impacting my ability to assess the strength of social bonds.

I also calculated 12 annual sociality measures for each male that were based on dyadic grooming indices. In the first of two methods (Figure S3.4; Appendix B), I calculated the dyadic grooming index as follows:

$$\frac{G_{i,j}}{TT_{i,j}}$$

where $G_{i,j}$ is the amount of time a dyad was observed grooming and $TT_{i,j}$ is the amount of time that the dyad was together in the same party and either member was the focal subject (Bray et al., 2016; Bray & Gilby, 2020; Machanda et al., 2013). Because this index may create a bias against individuals who choose to spend considerable amounts of time together, I also calculated a second dyadic grooming index as follows:

$$\frac{G_{i,j}}{OT_{i,j}}$$

where $G_{i,j}$ is the amount of time a dyad was observed grooming and $OT_{i,j}$ is the total observation time during which either member was the focal subject. I controlled for observation time because males are followed for different amounts of time. To minimize bias from poor sampling, I excluded male dyads from grooming analyses if $OT_{i,j}$ for a dyad was < 1800 minutes.

3.3.3 *Statistical Analyses*

Following prior work (Bray & Gilby, 2020), I fit all models using Hamilton Markov chain Monte Carlo (MCMC) with r-STAN v.2.19.13 (Stan Development Team, 2020) in R v.3.6.2 (R Core Team, 2019), using the *map2stan* function in the 'rethinking' package (McElreath, 2019). I explicitly specified the mathematical structure of all statistical models (https://github.com/joelbray/function-male-bonds). These models produce a specified number of estimates for the value of each parameter, which together create a posterior distribution for each parameter. By taking the mean, median, or standard deviation of these values, I can estimate the posterior mean, posterior median, and posterior standard deviation for each parameter. To make statistical inferences, I used tables of parameter estimates and plots of the posterior predictions. Although the sign and magnitude of the parameter estimates provide valuable information, plots of model predictions are also helpful for interpreting effects.

In all models, I used weakly informative priors for the fixed effects (Gelman et al., 2008). Weakly informative priors constrain parameter estimates to biologically plausible values, while allowing the information in the data to dominate information in the prior. Specifically, I set the means of the priors to 0 and the standard deviations to 2. I evaluated the quality of the models by visually inspecting the trace plots (McElreath, 2016, p. 253-254) and examining two numerical diagnostics. The first diagnostic, effective sample size, estimates the number of independent draws from the posterior distribution. Effective sample sizes that are substantially lower than the number of iterations in the chains indicate that the models are inefficient (McElreath, 2016, p. 257). The second, the Gelman-Rubin convergence diagnostic (Rhat), evaluates the convergence of different chains (Gelman & Rubin, 1992). Rhat values that deviate from 1.00 are cause for concern (McElreath, 2016, p. 257). All Rhat values were 1.00 and the number of effective sample sizes for all predictor variables were above 1900. I report both model diagnostics in Table S3.1 (Appendix B).

I standardized numeric predictor variables by centering and scaling the data (Schielzeth, 2010), with the exception of count variables. To center data, I subtracted the variable mean from each value, resulting in a mean of zero. To scale data, I then divided the newly centered data by its standard deviation. As a result, coefficients in these models indicate the change in the response variable associated with an increase in one standard deviation of the predictor variable (Bring, 1994; McElreath, 2016, p. 111). This procedure improves how well the model is fit to the data, increasing the accuracy of parameter estimates (McElreath, 2016, p. 111). Because the range of Elo scores changes over time, I standardized these scores within years. Some sociality indices varied predictably according to the number of adult males in the community in a given year; I did not standardize these variables by year, however, and instead addressed this by examining many predictors across my models, some of which account for variation in the number of adult males (e.g., a mean of dyadic indices).

I fit hierarchical normal models to estimate the annual change in mean Elo score for each adult male (current-year mean Elo score minus prior-year mean Elo score), standardized within years. Accordingly, the response variables represented the degree to which mean Elo scores increased or decreased compared to other males. One consequence of this standardization is that some males who had small increases in mean Elo score had negative standardized outcomes ($N = 29$ of 293 individual-years). This occurred when individual increases were small relative to the changes of other members in the community. The reverse (decreases in Elo scores having positive standardized values) never occurred. To verify that these cases did not influence the results, I ran every model with both unstandardized outcomes and outcomes standardized across the entire dataset instead of within years. The original response variable (standardized within years) was positively correlated to each of these alternative measures ($r = 0.88$; $p < 0.0001$; $N = 293$), and model results were unaffected.

In each model, except for two null models, the main predictor variable was a single prior-year sociality index. I included several covariates as well. Because males are expected to increase in dominance strength early in life, exhibit smaller changes in the middle of adulthood, and decrease in dominance strength later in life, I included prior-year age as a linear predictor. I also included prior-year mean Elo score because males with higher Elo scores are less likely to increase in Elo score and males with lower Elo scores are more likely to increase in Elo score. I included an interaction between prior-year age and prior-year mean Elo score because, for example, young males that have higher Elo scores are less likely to decrease in dominance strength than old males that have higher Elo scores. Because the effect of having strong social bonds might also vary according to male Elo score, I included an interaction between a male's prior-year mean Elo score and his prior-year sociality index. Lastly, I specified a varying intercept for male identity and included multiple varying slopes, allowing the effects of prior-year age, prior-year mean Elo score, and prior-year sociality to vary by male.

3.4 Results

I observed substantial variation in male-male social behavior across the study duration (Table S3.2 in Appendix B), reflecting changes in the demographic composition of the community, changes in the social behavior of the chimpanzees themselves, and observation intensity. Annual changes in mean Elo scores were also positively correlated with year-end changes in ordinal ranks ($r = 0.48$; $p < 0.0001$; $N = 332$).

Of the eight association models, all showed a positive relationship between the prior-year sociality index and annual change in mean Elo score (Table S3.1; Appendix B). Models based on dyadic indices generally had the best fit to the data, and the null model, without any sociality index, had the least weight (Table 3.2). Based on these comparisons, I report posterior means and standard deviations for parameters in the two best-fitting association models (Table 3.3). In the best-fit association model, males with a greater number of dyadic association indices above the mean (A5) were more likely to exhibit annual increases in mean Elo score (Fig. 3.1). On average, the difference between having ≤ 2 bonds above the mean versus having ≥ 4 bonds above the mean was the difference between exhibiting a decrease or increase in mean Elo score, respectively. Additionally, males with higher mean Elo scores were more likely to experience a decrease in mean Elo score in the following year (Figure S3.3; Appendix B).

Table 3.2

Model comparisons for models testing the effect of association indices on annual change in mean Elo score

Key	Model	WAIC	dWAIC	Weight
A5	Number of dyadic indices that are above the mean	722.88	0.00	0.50
A3	Sum of dyadic indices that are above the mean	723.02	0.14	0.47
A1	Sum of all dyadic indices	729.30	6.42	0.02
A2	Mean of all dyadic indices	733.33	10.45	0.00
A7	Proportion of arrivals with adult males	735.64	12.76	0.00
A4	Sum of dyadic indices that are ≥ 1 SD above the mean	737.80	14.92	0.00
A8	Mean number of adult males in each arrival	738.71	15.82	0.00
A6	Number of dyadic indices that are ≥ 1 SD above the mean	741.65	18.76	0.00
n/a	Null model (identical except no association index)	742.18	19.30	0.00

Note. Models with lower WAIC scores have better fits to the data, dWAIC values reflect the difference in WAIC between the best-fit model and a given model, and the weight reflects the relative likelihood of a model.

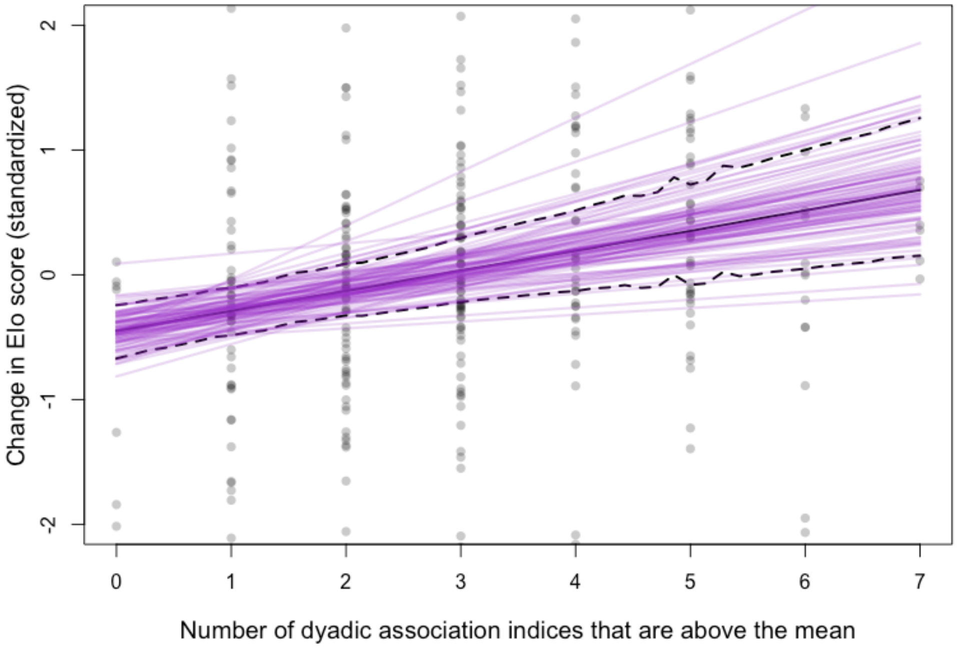
Table 3.3

Parameter estimates for the best-fitting models investigating the effect of association on annual change in mean Elo score

Key	Model	Parameter	Mean	SD
A5	Number of dyadic indices that are above the mean	Intercept	-0.39	0.13
		Age	-0.24	0.07
		Mean Elo score (dominance)	-0.44	0.16
		Sociality index	0.16	0.04
		Dominance X Age	-0.28	0.10
		Dominance X Sociality index	0.01	0.04
A3	Sum of dyadic indices that are above the mean	Intercept	0.07	0.09
		Age	-0.23	0.07
		Mean Elo score (dominance)	-0.45	0.11
		Sociality index	0.24	0.06
		Dominance X Age	-0.28	0.11
		Dominance X Sociality index	0.05	0.06

Figure 3.1

Posterior predictions for the influence of the number of dyadic association indices that are above the mean on annual change in mean Elo score



Note. Posterior predictions for the influence of the number of dyadic association indices that are above the mean (A5) on annual change in mean Elo score. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions. Grey dots are raw data.

Of the 16 grooming models, models with dyadic grooming indices that controlled for observation time generally had higher weights (Table 3.4) and more positive relationships with annual changes in mean Elo scores (Table S3.1; Appendix B) than the models with dyadic grooming indices that controlled for time together. The four measures based on the proportion of time spent grooming showed somewhat positive relationships with change in mean Elo score; these models, however, did not receive any weight in the model comparisons, nor did the null model without any sociality index. I report posterior means and standard deviations for parameters in the best-fitting grooming models in Table 3.5. In the best-fit grooming model (G8), males with higher mean grooming indices, controlling for observation time, were more likely to exhibit increases in mean Elo score in subsequent years (Fig. 3.2). Whereas males with average grooming indices experienced no consistent changes in mean Elo scores, males whose indices were two or three times the average typically experienced increases in mean Elo scores. This effect was not as robust as in the association models, however, as indicated by a larger posterior standard deviation relative to the posterior mean.

Table 3.4

Model comparisons for models testing the effect of grooming indices on annual change in mean Elo score

Key	Model	WAIC	dWAIC	Weight
G8	Mean of all dyadic indices (observation time)	750.72	0.00	0.55
G7	Sum of all dyadic indices (observation time)	753.09	2.37	0.17
G2	Mean of all dyadic indices (time together)	753.62	2.90	0.13
G9	Sum of dyadic indices that are above the mean (observation time)	753.98	3.26	0.11
G1	Sum of all dyadic indices (time together)	757.22	6.50	0.02
G3	Sum of dyadic indices that are above the mean (time together)	758.02	7.30	0.01
G10	Sum of dyadic indices that are ≥ 1 SD above the mean (observation time)	761.20	10.48	0.00
G12	Number of dyadic indices that are ≥ 1 SD above the mean (observation time)	764.71	13.99	0.00
G11	Number of dyadic indices that are above the mean (observation time)	767.34	16.62	0.00
G16	Proportion of time grooming with adult males (receive)	769.90	19.18	0.00
G14	Proportion of time grooming with adult males (mutual)	771.10	20.39	0.00
n/a	Null model (identical except no grooming index)	771.45	20.73	0.00
G13	Proportion of time grooming with adult males (total)	771.51	20.80	0.00
G15	Proportion of time grooming with adult males (give)	771.92	21.20	0.00
G4	Sum of dyadic indices that are ≥ 1 SD above the mean (time together)	772.04	21.32	0.00
G5	Number of dyadic indices that are above the mean (time together)	773.37	22.65	0.00
G6	Number of dyadic indices that are ≥ 1 SD above the mean (time together)	774.11	23.39	0.00

Note. Models with lower WAIC scores have better fits to the data, dWAIC values reflect the difference in WAIC between the best-fit model and a given model, and the weight reflects the relative likelihood of a model. For clarity, I note in parentheses whether the dyadic grooming index in a particular model controlled for time together or only observation time.

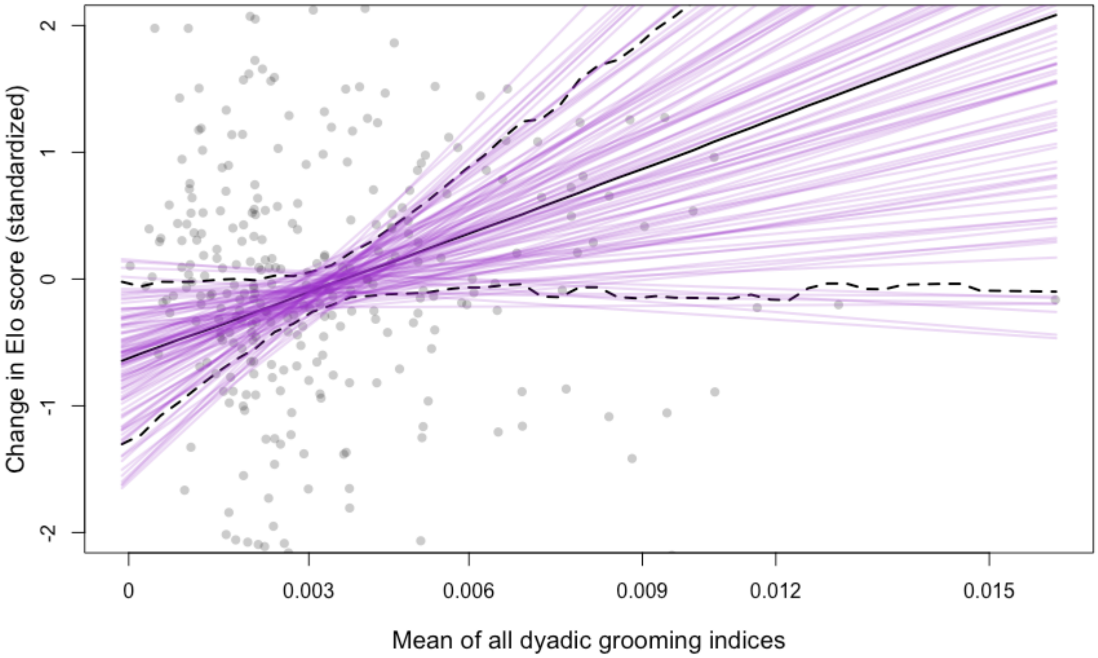
Table 3.5

Parameter estimates for the best-fitting models investigating the effect of grooming on annual change in mean Elo score

Key	Model	Parameter	Mean	SD
G8	Mean of all dyadic indices, controlling for observation time	Intercept	0.00	0.09
		Age	-0.27	0.09
		Mean Elo score (dominance)	-0.49	0.11
		Sociality index	0.16	0.11
		Dominance X Age	-0.28	0.11
		Dominance X Sociality index	0.00	0.09
G7	Sum of all dyadic indices, controlling for observation time	Intercept	-0.01	0.09
		Age	-0.27	0.08
		Mean Elo score (dominance)	-0.50	0.11
		Sociality index	0.15	0.09
		Dominance X Age	-0.27	0.11
		Dominance X Sociality index	0.16	0.07

Figure 3.2

Posterior predictions for the influence of the mean of all dyadic grooming indices on annual change in mean Elo score



Note. Posterior predictions for the influence of the mean of all dyadic grooming indices (G8) on annual change in mean Elo score. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions. Grey dots are raw data.

3.5 Discussion

Among adult male chimpanzees at Gombe National Park, strong bonds were positively associated with annual changes in mean Elo scores, which are a measure of dominance strength. Annual changes in mean Elo scores were themselves positively correlated with year-end changes in ordinal rank. Given previous findings that higher rank generally improves male chimpanzee reproductive success (Boesch et al., 2006; Inoue et al., 2008; Langergraber et al., 2013; Newton-Fisher et al., 2010; Wroblewski et al., 2009), including at Gombe, results suggest that the formation and maintenance of strong social bonds lead to adaptive benefits. The most likely mechanism can be inferred from previous research on chimpanzees: affiliative social interactions and coalition frequency are correlated (Mitani, 2006; Watts, 2002), and participation in strategic coalitions is associated with increases in rank and paternity success (Gilby et al., 2013). This study thus fills a gap in prior work by suggesting that behaviors involved in the formation and maintenance of social bonds, which do not result in immediate changes in dominance rank, are nonetheless a valuable investment. These findings also support the hypothesis that same-sex social bonds in males evolved to help individuals compete for dominance status (Ostner & Schülke, 2014).

A recent 34-year study of Gombe chimpanzees, however, found that high rank only leads to increased paternity success for the alpha male; other than the alpha, males did not differ in their siring success on the basis of ordinal rank (Feldblum et al., under review). This differs from an earlier study of paternity in this population based on fewer paternities (Wroblewski et al., 2009) and complicates the story. Because most increases in mean Elo score do not lead to acquisition of alpha status, what are the benefits of strong social bonds? First, small increases in Elo score and ordinal rank are beneficial if they culminate over time in becoming alpha. Of the 36 males that reached adulthood in the Kasekela community, 12 (33%) achieved alpha status. Second, even for males that never achieve alpha status, additional benefits may include increased access to resources

(Hall & Fedigan, 1997; Post et al., 1980), lower glucocorticoid levels (Gesquiere et al., 2011; reviewed in: Sapolsky, 2005), or greater longevity. Any benefits that accrue over the long-term would not be captured by cross-sectional studies of rank (Feldblum et al., under review). Third, given the number of studies from other chimpanzee communities pointing to relationships between rank and reproductive success (Boesch et al., 2006; Inoue et al., 2008; Langergraber et al., 2013; Newton-Fisher et al., 2010), this could be a phenomenon unique to Gombe, in which case males at Gombe may be pursuing an evolved strategy that has not been successful in recent history. Fourth, future studies of the Gombe chimpanzees that analyze larger samples could demonstrate that high-ranking males other than the alpha achieve more reproductive success than males lower in the hierarchy. Ultimately, given that male chimpanzees invest substantial energy and time into rank acquisition (Goodall, 1986; Kaburu et al., 2013; Mitani, 2009b; Muller & Mitani, 2005), further study of the benefits of rank is warranted.

In the present study, the relationship between sociality and changes in dominance strength was consistent across models that included a sociality index based on party-level associations. This relationship, however, was more variable in models that included a sociality index based on grooming activity: models with dyadic grooming indices that controlled for observation time were positively associated with changes in dominance strength, whereas models with dyadic grooming indices that controlled for time together in parties did not predict changes in dominance strength. This is somewhat surprising, given that the latter indices were associated with increased mating success in previous studies (Bray et al., 2016), but it suggests that dyadic grooming indices that controlled for observation time and not time together were more predictive because males were spending time together in order to groom. Particularly in species with high fission-fusion dynamics like chimpanzees (Aureli et al., 2008), time spent together is a key component of male social relationships (Bray & Gilby, 2020; Gilby & Wrangham, 2008; Newton-Fisher, 1999).

More broadly, studies have documented a consistent relationship between male dominance and reproductive success in primates (reviewed in: Cowlishaw & Dunbar, 1991; De Ruiter & Van Hooff, 1993; Fedigan, 1983; Ostner et al., 2008) and other taxa (reviewed in: Ellis, 1995), which suggests that indirect effects between social bonds and adaptive outcomes, like what I believe is occurring in male chimpanzees, may be essential components of fitness. This is particularly likely in primates, cetaceans, and social carnivores, which generally have complex social structures. For example, male Assamese macaques with stronger social bonds are more likely to rise in rank and reproduce (Schülke et al., 2010). This relationship is also not unique to males. In female yellow baboons and spotted hyenas (*Crocuta crocuta*), social bonds with maternal kin are essential for rank inheritance (Engh et al., 2000; Hausfater et al., 1982; Holekamp & Smale, 1991; Lea et al., 2014). High female rank in these species increases access to limited resources and confers a variety of benefits, including faster infant growth (Altmann & Alberts, 2005; Hofer & East, 2002), shorter interbirth intervals (Cheney et al., 2004), and, eventually, higher reproductive success (Hofer & East, 2002; Holekamp, Smale, & Szykman, 1996; reviewed in: Silk, 2002).

How widely this phenomenon exists remains to be determined. Chimpanzees are long-lived (Hill et al., 2001; Muller & Wrangham, 2013; Wood et al., 2017) and can afford to invest in affiliative relationships throughout their lives (Goodall, 1986; Rosati et al., 2020), with benefits accruing over the long-term. Large body size is also useful but not essential for achieving high rank (Foster et al., 2009; Goodall, 1986; Pusey et al., 2005). By contrast, in a study of Guinea baboons (*P. papio*), males with stronger male-male bonds sired fewer offspring (Dal Pesco, 2019), reflecting a possible tradeoff between time spent with males and time spent with females. Similarly, in a study of bighorn sheep (*Ovis canadensis*), social network centrality had no effect on male offspring production (Vander Wal et al., 2015). Together, these studies suggest that positive relationships between social bonds and adaptive outcomes are less likely in species that are shorter-lived or in which body size and strength are more predictive of dominance.

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CHAPTER 4

IMMATURE MALE CHIMPANZEES’ SOCIAL RELATIONSHIPS WITH ADULT MALES, BUT NOT PEERS, PERSIST INTO ADULTHOOD

4.1 Abstract

Highly differentiated and affiliative social relationships are observed in a variety of mammals, including primates, cetaceans, and social carnivores. While there has been a transformation in our understanding of the form and function of social bonds in the last two decades, the role of early life social experiences in the development of bonds remains less clear. Few studies have examined whether social relationships during infancy and juvenility (aside from those between mothers and offspring) persist into adulthood. In this study, I used longitudinal data on wild chimpanzees (*Pan troglodytes schweinfurthii*) at Gombe National Park, Tanzania, to investigate the effects of association during infancy and juvenility (hereafter immaturity) on adult male social bonds. I used maternal associations as proxies for the associations of immature males. I found that immature males who associated with adult males at higher rates had stronger bonds with those same adult males later in life. By contrast, rates of association between immature males were not correlated with dyadic bond strength as adults. Overall, these findings emphasize the importance of early socialization and maternal effects in male chimpanzee social development. These results also reinforce previous studies in mountain gorillas (*Gorilla beringei*) and bottlenose dolphins (*Tursiops sp.*), suggesting that the persistence of social relationships in the absence of maternal ties may be more likely to evolve in long-lived species where young adult males face challenges entering an adult hierarchy comprised of stronger and/or more socially experienced competitors.

4.2 Introduction

In several mammalian taxa, including primates, cetaceans, and social carnivores, socioecological conditions that facilitate social tolerance and frequent interaction between individuals have favored the evolution of highly differentiated and affiliative social bonds, which promote cooperation and confer fitness benefits (reviewed in: Hruschka & Silk, 2017; Ostner & Schulke, 2018; Seyfarth & Cheney, 2012; Silk, 2007). Strong social bonds have been linked to adaptive benefits in yellow and chacma baboons (*Papio cynocephalus* and *P. ursinus*) (Archie et al., 2014; Cheney et al., 2016; Silk et al., 2003, 2009, 2010b), feral horses (*Equus caballus*) (Cameron et al., 2009), bottlenose dolphins (*Tursiops* sp.) (Frère et al., 2010; Stanton & Mann, 2012), Assamese macaques (*Macaca assamensis*) (Schülke et al., 2010), and chimpanzees (*Pan troglodytes*) (Chapter 3; Feldblum et al., under review).

Despite all I know about the form and function of mammalian social bonds, the role of early life social experiences in the development of these bonds remains unclear. The prolonged period of development in primates and other long-lived and socially complex species is hypothesized to be critical to social skill development (Joffe, 1997; Lonsdorf & Ross, 2012), but this period may also serve as an opportunity in invest in long-term social relationships. In several species, relationships persist from infancy into adolescence and adulthood, but they are almost entirely composed of maternal kin. For example, in female philopatric yellow and chacma baboons, mothers and daughters form the strongest and most stable social bonds (Silk et al., 2010a, 2012; Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006). Likewise, in species characterized by male philopatry, such as bonobos (*Pan paniscus*), or those in which both sexes remain in their natal groups, such as orcas (*Orcinus orca*), sons can form stable relationships with their mothers that persist into adulthood (bonobos: Furuichi, 2009; Surbeck et al., 2019; Surbeck, Mundry, & Hohmann, 2011; orcas: Brent et al., 2015; Foster et al., 2012; Rose, 1992).

Aside from mother-offspring dyads, however, it remains less clear whether social relationships in mammals persist across developmental stages. Among males, immature individuals could pursue two strategies that are not mutually exclusive. One, immature males could invest in relationships with adult males. Two, immature individuals could forge relationships with similarly aged peers. Studies of mountain gorillas (*Gorilla beringei beringei)* provide the strongest evidence of persistent relationships with adult males. Immature mountain gorillas form close relationships with adult males (Rosenbaum et al., 2011), and adult male dominance rank is a stronger predictor of relationship strength during the immature period than either paternity or age difference (Rosenbaum, Hirwa, Silk, Vigilant, et al., 2015). These social relationships are stable across developmental stages, with juvenile proximity to adult males predicting proximity relationships in adolescence and young adulthood (Rosenbaum, Hirwa, Silk, & Stoinski, 2015). Enduring relationships may benefit younger males by providing mating opportunities with nearby females, reducing the likelihood of aggression from adult competitors, and/or helping them to gain a foothold in the adult male dominance hierarchy (Rosenbaum, Hirwa, Silk, & Stoinski, 2015). By contrast, studies of bottlenose dolphins (*Tursiops* sp.), in which adult male reproductive success depends on both competitive ability and alliance formation (Connor, 2007; Connor et al., 2001; Connor & Krützen, 2015), provide strong evidence of persistent relationships between peers. In a recent study, Gerber et al. (2020) found that social bonds among male bottlenose dolphins during adolescence predicted alliance partners in adulthood. Together, these studies demonstrate that social bonds among non-maternal kin can persist across developmental stages, but data on whether this phenomenon exists in a wider variety of mammalian species are necessary to reveal the underlying socioecological factors that favor its evolution.

Chimpanzees present an opportunity to investigate the persistence of social relationships across developmental stages. First, adult male chimpanzees form some of the strongest and most stable social bonds among mammals (Bray & Gilby, 2020; Gilby & Wrangham, 2008; Mitani, 2009a). Maternal brothers generally form the strongest bonds, but, because of demographic constraints, most close and enduring relationships are formed between unrelated or distantly related individuals (Bray & Gilby, 2020; Langergraber et al., 2007; Mitani, 2009a), and few factors explain variation in bond strength among non-kin (Bray & Gilby, 2020; Langergraber et al., 2007). Male-male social bonds and cooperative interactions are useful in several contexts, leading to higher rank, increased mating access, and greater paternity success (Chapter 3; Bray, Pusey, & Gilby, 2016; Duffy, Wrangham, & Silk, 2007; Feldblum et al., under review; Gilby et al., 2013; Goodall, 1986; Mitani, 2009b; Muller & Mitani, 2005; Watts, 1998).

Second, chimpanzees exhibit a prolonged period of development. Infant chimpanzees are typically weaned between the ages of 3-5 years but continue to travel with their mother for an additional 4-5 years (Bray et al., 2017; Goodall, 1986; Lonsdorf et al., 2019). Male chimpanzees also remain in their natal community for life (Goodall, 1986). As a result, immature males may take advantage of the prolonged developmental period by forging bonds that continue into adulthood. In a prior study at Gombe National Park, Tanzania, three adolescents' association preferences for particular adult males appeared to persist into adulthood, including one non-sibling pair (Pusey, 1990). Similarly, in the Ngogo community in Kibale National Park, Uganda, infant and juvenile associations with adult males during a single year of their development explained variation in association among those dyads after the younger males entered adulthood (Sandel, 2017).

Third, the high fission-fusion dynamics of chimpanzees can help us better understand the socioecological factors involved in the persistence of social relationships across developmental stages. Unlike baboons and mountain gorillas, which form relatively cohesive social groups, chimpanzee communities are characterized by high fission-fusion dynamics (Aureli et al., 2008), in which subgroup size and composition can change throughout the day (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1990). Whereas adult males are highly gregarious (Goodall, 1986; Mitani, 2009b; Pepper et al., 1999), adult females more often associate with only dependent offspring (Goodall, 1986; Pusey, 1990; Williams et al., 2002), although there is substantial variation between and within populations and subspecies (Foerster et al., 2015; Gilby & Wrangham, 2008; Langergraber et al., 2009; Lehmann & Boesch, 2009; Machanda et al., 2013). As a result, maternal association patterns largely determine offspring social opportunities throughout infancy and juvenility, and immature individuals vary widely in the extent to which they are exposed to adult males and male peers (Foerster et al., 2015; Goodall, 1986; Machanda et al., 2016; Murray et al., 2014; Pusey, 1983; Williams et al., 2002). Although prior studies suggest that early socialization is important for the development of social skills in wild chimpanzees, the degree to which early social experiences are important for the development of social relationships is unknown.

Using longitudinal data from Gombe National Park, Tanzania, I investigate the relationship between early life social experiences and adult male social bonds in wild chimpanzees. First, I examine whether maternal association patterns with adult males during an offspring's infancy and juvenility (hereafter immaturity) predict the strength of the offspring's social bonds with the same adult male partners during adulthood. Second, I explore whether maternal associations with the mothers of other immature males, which create opportunities for male peers to interact, predict the strength of adult male bonds.

4.3 Methods

4.3.1 *Study Site, Subjects, and Data Collection*

I studied chimpanzees (*P. t. schweinfurthii*) in the Kasekela community in Gombe National Park, Tanzania, which is located on the eastern shore of Lake Tanganyika. The park consists of 35 km^2 of evergreen riverine forest, deciduous woodland, and grassland (Clutton-Brock & Gillett, 1979). Observations of the Kasekela community began in 1960, and chimpanzees were fully habituated by 1966 through the use of banana provisioning at a feeding station (Goodall, 1986; Wilson, 2012). Feeding continued at low levels until 2000 (Wilson, 2012). Since 1973, Tanzanian field assistants have conducted full-day focal observations (Altmann, 1974) of chimpanzees in this community (Wilson, 2012). Teams of two observers follow all chimpanzees that travel independently of their mothers approximately once per month. During focal follows, one observer records party composition, specifying when individuals join and leave the focal chimpanzee's party. Two individuals are considered to have 'arrived' together if they either (i) are present in a party at the start of a focal follow or (ii) join a party within five minutes of each other. A second observer records a continuous narrative of the behavior of the focal chimpanzee, including all occurrences of grooming behavior and conspicuous activities of non-focal individuals, such as submissive pant-grunt vocalizations. A relational database, including both behavioral and demographic data, is maintained by the Gombe Research Consortium and coordinated by the Institute of Human Origins at Arizona State University.

4.3.2 *Analyses*

I examined behavioral data from 1970 to 2015, investigating whether developmental variables explain variation in the strength of adult male social relationships, above and beyond the factors identified in a previous study on the form of adult male social bonds at Gombe (Bray & Gilby, 2020). Following prior studies, I classified males as adults if they were ≥ 16 years old (Bray & Gilby, 2020; Goodall, 1986; Mitani, 2009a; Sandel et al., 2016). The birthdates of 19 males born in the Kasekela community after the study began were estimated based on both their size and appearance when first observed as well as the dates of previous sightings of the mother without the infant (Strier et al., 2010). The median difference between the minimum and maximum birthdates was 7 days (Mean ± SD = 8.3 ± 9.2, $N = 19$). Of these 19 males, I had paternity data for only six, so I did not include paternity as a predictor variable in statistical models. For four remaining males that were included only as the older adult male in a dyad, birthdates were estimated based on morphological characteristics and familial relationships; the median number of days between the estimated minimum and maximum birthdates was 548 days (Mean ± SD = 548 ± 211 days, $N = 4$).

(i) Dominance

I identified all pant-grunt vocalizations (formal and unambiguous signals of submission in chimpanzees: Bygott, 1979; Goodall, 1986) between males that were observed at the feeding station or during focal follows. I only included pant-grunts with clear actors and recipients, which included interactions when multiple chimpanzees pant-grunted to one individual but not vice versa. I used these interactions to calculate Elo ratings (Albers & de Vries, 2001), which estimate a subject's dominance on any given date while accounting for demographic changes and missing data (Neumann et al., 2011). To calculate Elo scores on each day of the study period, I used a maximum-likelihood implementation of the Elo method using the 'EloOptimized' package (Feldblum et al., 2019; Foerster et al., 2015) in R v.3.6.2 (R Core Team, 2019). To estimate annual dominance scores for each male, I calculated mean daily Elo scores across each year (Bray & Gilby, 2020).

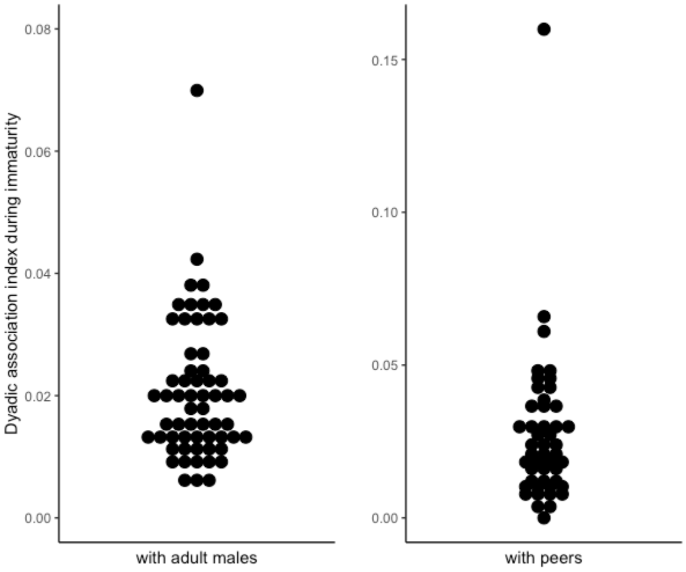
(ii) Associations of Immature Males

To estimate the social exposure of immature males to both adult males and peers, I used maternal associations as a proxy because immature individuals, particularly those that were still traveling with their mothers, were not systematically recorded independently in the long-term behavioral data. I examined association patterns between mothers and adult males (representing immature male and adult male associations: Fig.

4.1) and between mothers and other mothers (representing peer associations: Fig. 4.1). This study focused on the association patterns of immature males between the ages of 1 and 8 years, which spans the infant and juvenile periods. During this developmental period, young chimpanzees largely remain in their mother's party but are comfortable leaving their mother's side to interact independently with others (Goodall, 1986; Pusey, 1983).

Figure 4.1

Distribution of dyadic association indices between immatures with adult males and peers



To assess association patterns between immature and adult males, I extracted association data during the period in which the subject was between 1 and 8 years and the adult male was ≥ 16 years. I included dyads that had ≥ 1 year of association data from the younger male's immature period (range: 431 – 2556 days). To assess association patterns of immature dyads, I extracted association data during the period in which both individuals were between 1 and 8 years old. Again, I included dyads that had ≥ 1 year of association data during immaturity (range: 369 – 2473 days). Because of these criteria, if two males were between 7 and 9 years apart in age, they were excluded from both sets of analyses.

The dyadic association index was based on joint arrivals (see above) in a party by the subject's mother and each adult male or other mother in the community (Foerster et al., 2015; Murray et al., 2006; Williams et al., 2002). This index is positively correlated with indices based on the proportion of time spent together (Bray & Gilby, 2020). To avoid non-independent arrivals from individuals leaving and joining a subgroup throughout the day, I considered only the first arrival of an individual per day. I also restricted the data to include only arrivals of four adults or fewer (Bray & Gilby, 2020) because associations of large numbers of individuals are more likely to reflect grouping for reasons other than social preference, such as a high-quality food resource or a female in estrous (Matsumoto-Oda et al., 1998; Mitani, Watts, & Lwanga, 2002). Social preference matters because immature males are more likely to be in proximity to and interact with specific adults when their mothers are themselves in proximity to and interacting with those individuals (author name redacted, unpublished data). To be classified as an adult and included in the analysis of arrivals, females had to be either a mother with a son older than 1 year or be ≥ 15 years old, the mean age at first birth at Gombe (Walker et al., 2018). In my dataset, only one mother was included before she was 15 years old; she was 12.9 at the birth of her first son.

After preparing the association data, I calculated the DAI as follows:

$$\frac{J_{x,y}}{A_x + A_y - J_{x,y}}$$

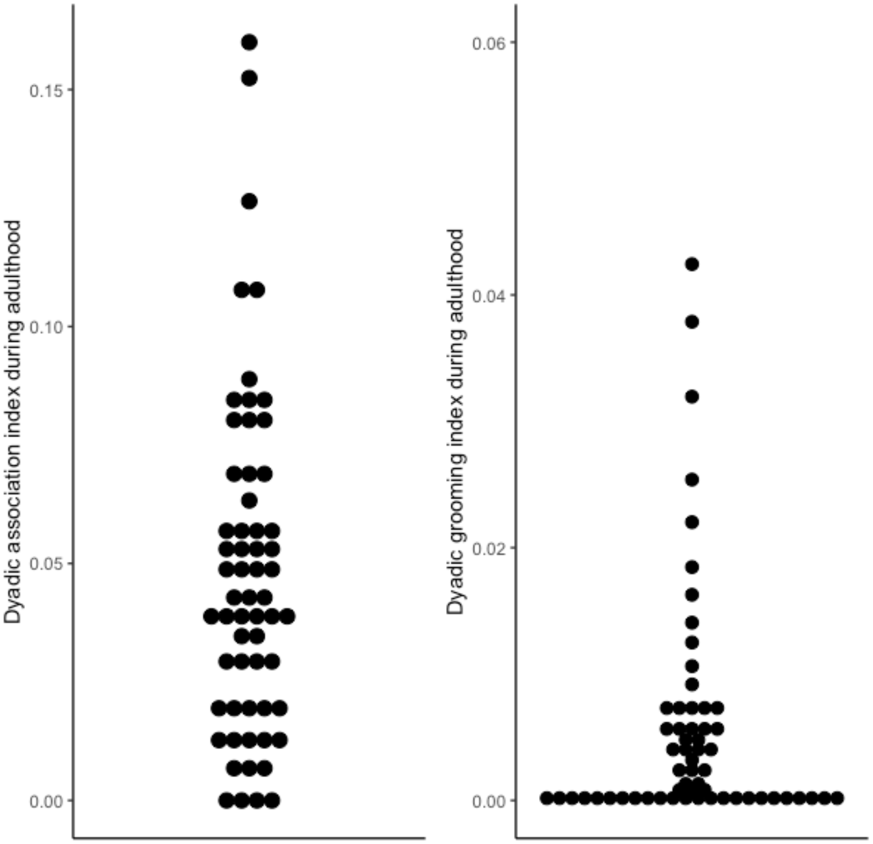
where $J_{x,y}$ is the number of joint arrivals for each dyad, A_x is the total number of arrivals for the mother, and A_y is the total number of arrivals of the adult partner (Cairns & Schwager, 1987). Because $J_{x,y}$ can vary slightly within dyads depending on arrival times (e.g., a mother might arrive jointly with another individual but, depending on the number of chimpanzees arriving within 5 minutes of each individual's arrival, the same might not be true for the other individual), each peer dyad had two highly similar DAIs (Pearson's correlation: $r = 0.999$, $N = 47$ dyads, $P < 0.0001$). I calculated the mean of these two indices in order to obtain a single DAI for each peer dyad. For DAIs between mothers and adult males, I used the DAI from the mother's perspective.

(iii) Adult Male Bond Strength

To assess the strength of adult male-male ("male", hereafter) social bonds, I calculated two annual indices, one based on party-level association and one on grooming (Fig. 4.2), both of which I define below. These behaviors are standard for assessing adult male social bonds in chimpanzees (Gilby & Wrangham, 2008; Goodall, 1986; Mitani, 2009b; Newton-Fisher, 1999; Samuni et al., 2018).

Figure 4.2

Distribution of adult-adult association indices and grooming indices



To measure party-level association, I calculated a DAI in the same manner as described above, except that all females had to be ≥ 15 years old to be included in arrivals. I further eliminated all dyads from the analysis for which at least one of the two male members had 20 or fewer arrivals in a given year, eliminating bias from indices that would otherwise have been based on a small number of data points (Bray & Gilby, 2020; Foerster et al., 2015). I also calculated an annual dyadic grooming index as follows: the amount of time a dyad was observed grooming divided by the total observation time in which the members were both present in the same party and either member was the focal subject (Bray & Gilby, 2020; Machanda et al., 2013; Silk et al., 2013). I limited my analysis to dyads that were together in parties in any given year for ≥ 1800 minutes. This ensured that data would not be biased by dyads that were rarely together but groomed frequently when they did associate (Bray et al., 2016; Bray & Gilby, 2020).

4.3.3 *Statistical analyses*

All statistical models had a non-directional dyadic response variable, with both individuals and dyads repeated across rows in the data. Because the individual identities of the members of each dyad were stored in separate columns, traditional statistical methods would estimate two discrete varying effects. To solve this problem, I used multiple indexing notation to estimate a single varying intercept from the two columns of individual identities (Bray & Gilby, 2020; Silk et al., 2017). A separate varying effect was specified for the dyad. I also explicitly specified the mathematical structure of all statistical models (https://github.com/joelbray/development-male-bonds).

I fit all models using Hamilton Markov chain Monte Carlo (MCMC) with r-STAN v.2.19.13 (Stan Development Team, 2020) in R v.3.6.2 (R Core Team, 2019), using the map2stan function in the ‘rethinking’ package (McElreath, 2019). When these models are executed, they produce a user-specified number of estimates for the value of each parameter, which together create a posterior distribution for each parameter. By taking the mean, median, or standard deviation of these values, I can estimate the posterior mean, posterior median, and posterior standard deviation for each parameter. Although the sign and magnitude of the parameter estimates provides some information to make statistical inferences, I also made plots of the model predictions, which is particularly helpful for interpreting effects from mixture models that combine multiple distributions (see below).

In all models, I used a hierarchical zero-augmented gamma distribution, which combines a Bernoulli and gamma distribution. The Bernoulli component uses a logit link and estimates *p*, the probability of observing an outcome of 0. For all outcomes > 0, the gamma component estimates the mean, λ, and a shape parameter, *k*. The joint likelihood is calculated by multiplying the likelihoods of each distribution together and converting them to a real scale using their link functions (Silk et al., 2017). Negative regression coefficients in the Bernoulli component (β_z) signify a lower probability of observing an outcome of zero, while positive regression coefficients in the gamma component (β_g) signify larger outcomes.

I used weakly informative priors for the fixed effects (Gelman et al., 2008). Weakly informative priors constrain parameter estimates to biologically plausible values, while allowing the information in the data to dominate information in the prior. Because I standardized all numeric predictor variables, I set the mean to 0 and the standard deviation to 2. I evaluated the quality of the models by visually inspecting the trace plots (McElreath, 2016, p. 253-254) and examining two numerical diagnostics. The first diagnostic, effective sample size, estimates the number of independent draws from the posterior distribution. Effective sample sizes that are substantially lower than the number of iterations in the chains indicate that the models are inefficient (McElreath, 2016, p. 257). The second, the Gelman-Rubin convergence diagnostic (Rhat), evaluates the convergence of different chains (Gelman & Rubin, 1992). Rhat values that deviate from 1.00 are cause for concern (McElreath, 2016, p. 257). In this study, all Rhat values were

1.00, and the effective sample sizes for all predictor variables were above 1000 (Appendix C).

As described above, I standardized all numeric predictor variables by centering and scaling the data (Schielzeth, 2010). Consequently, coefficients in the models indicate the change in the response variable associated with an increase in one standard deviation of the predictor variable (Bring, 1994; McElreath, 2016, p. 111). This procedure also improves how well the model is fit to the data, increasing the accuracy of parameter estimates (McElreath, 2016, p. 111). I did not standardize binary variables.

(i) Immature Associations with Adult Males

I examined the effect of immature associations with adult males on subsequent adult male social bonds (i.e., after the immature male became an adult). The response variable in one model was the dyadic association index, whereas in the other it was the dyadic grooming index. Each model inherited all annual predictor variables from a previous study (Bray & Gilby, 2020): age and rank for each individual, age difference, rank difference, maternal kinship (whether the members of a dyad were maternal brothers), and interactions between maternal kinship and both age difference and rank difference. In the present study, I added two additional predictor variables: the dyadic association index during the immature period and the number of days on which this index was based. I specified varying intercepts for subject identity, dyad identity, and year. Because individual age, individual rank, and dyadic rank difference all varied across years, and their effects on bond strength might vary by individual and dyad, I also specified varying slopes for these effects.

(ii) Associations Between Immature Peers

I examined the effect of associations between immature peers on adult male social bonds (i.e., after both immature males became adults), running models that were identical in structure and kind to the models described above except that they excluded maternal brothers. I excluded maternal brothers because maternal siblings were always together during immaturity according to my association index, which meant that their indices were extreme outliers compared to the rest of the dataset.

4.4 Results

In 10.8% of cases, a subject's strongest adult bond in a given year was with the adult male with whom he associated most frequently during immaturity. By contrast, 6.9% of males' strongest adult bonds in a given year were with the peer with whom he associated most frequently during immaturity.

Immature males that had higher association indices with adult males both associated more frequently ($\beta_z = -1.14 \pm 0.76$, $\beta_g = 0.09 \pm 0.06$; Table 4.1) and groomed at higher rates ($\beta_z = -0.46 \pm 0.43$, $\beta_g = 0.18 \pm 0.09$; Table 4.1) with those same older, adult males after they became adults themselves. This is illustrated by the positive correlation visible in Figures 3.3 and 3.4, the negative regression coefficients in the Bernoulli components (β_z), and the positive regression coefficients in the gamma components (β_g). Importantly, the posterior standard deviations are also smaller than the posterior means. For example, the strongest relationship that persisted was between GB and ST, a pair of males who were frequently together in parties when GB was immature and continued to interact after GB became an adult. Additionally, there was no effect of maternal sibship in either model, unlike the previous study (Bray & Gilby, 2020). These models were distinct from previous ones because they did not include males close in age, reinforcing the prior study's finding that the effects of maternal kinship on adult male bonds were strongest among males of similar ages.

Table 4.1

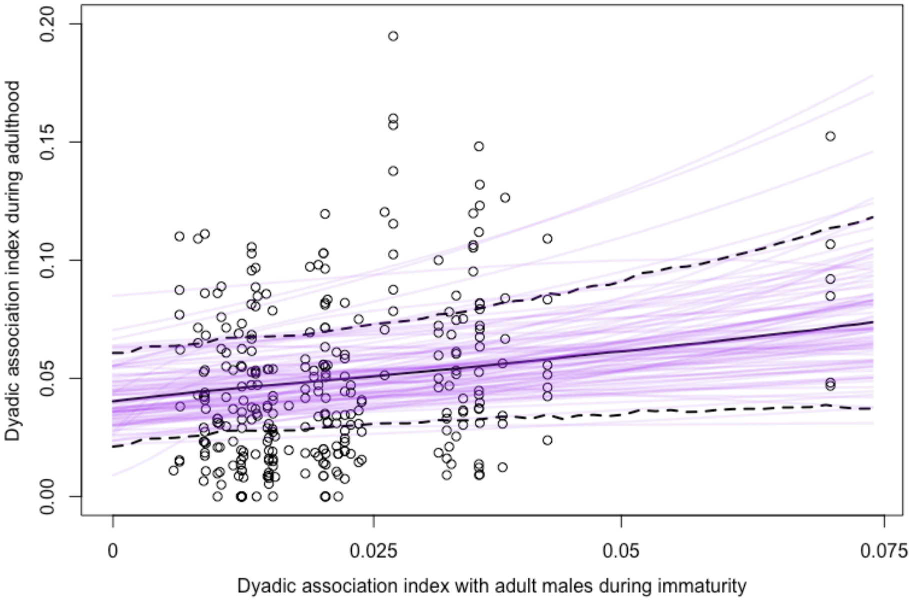
Parameter estimates for adult male models

Model	Parameter	Mean	SD
Outcome: Association **Predictor:** Association with Adult Males while Immature	α_z Intercept	-1.65	1.34
	α_g Intercept	-2.99	0.23
	β_z Rank	-0.81	0.49
	β_g Rank	0.04	0.05
	β_z Age	0.60	0.43
	β_g Age	-0.08	0.05
	β_z Maternal kinship	-0.76	1.82
	β_g Maternal kinship	-0.13	0.42
	β_z Rank difference	-0.25	0.56
	β_g Rank difference	0.05	0.06
	β_z Age difference	-3.11	1.07
	β_g Age difference	-0.07	0.15
	β_z Maternal kinship X age difference	-0.97	1.68
	β_g Maternal kinship X age difference	0.10	0.24
	β_z Maternal kinship X rank difference	0.20	1.83
	β_g Maternal kinship X rank difference	-0.79	0.24
	β_z Association while immature	-1.14	0.76
	β_g Association while immature	0.09	0.06
	β_z Joint days during target window	1.44	0.69
	β_g Joint days during target window	-0.03	0.10
	Observations (N)	*306*	
	Dyads (N)	*60*	
	Individuals (N)	*23*	
Outcome: Grooming **Predictor:** Association with Adult Males while Immature	α_z Intercept	-1.88	0.97
	α_g Intercept	-4.51	0.36
	β_z Rank	-0.29	0.30
	β_g Rank	0.06	0.09
	β_z Age	-0.61	0.29
	β_g Age	0.23	0.07
	β_z Maternal kinship	-1.57	1.56
	β_g Maternal kinship	-0.11	0.66
	β_z Rank difference	0.12	0.36
	β_g Rank difference	0.04	0.08
	β_z Age difference	0.12	0.64
	β_g Age difference	-0.17	0.24
	β_z Maternal kinship X age difference	0.84	0.92
	β_g Maternal kinship X age difference	-0.02	0.37
	β_z Maternal kinship X rank difference	1.04	1.14
	β_g Maternal kinship X rank difference	-0.61	0.30
	β_z Association while immature	-0.46	0.43
	β_g Association while immature	0.18	0.09
	β_z Joint days during target window	0.48	0.49
	β_g Joint days during target window	-0.21	0.16
	Observations (N)	*295*	
	Dyads (N)	*60*	
	Individuals (N)	*23*	

Note. All parameters with a subscript of z correspond with the Bernoulli component of the model, while those with a subscript of g correspond with the gamma component. Negative coefficients in the Bernoulli component indicate a lower probability of observing dyadic indices of zero, while positive values in the gamma component indicate parameters that are associated with higher dyadic indices and stronger bonds.

Figure 4.3

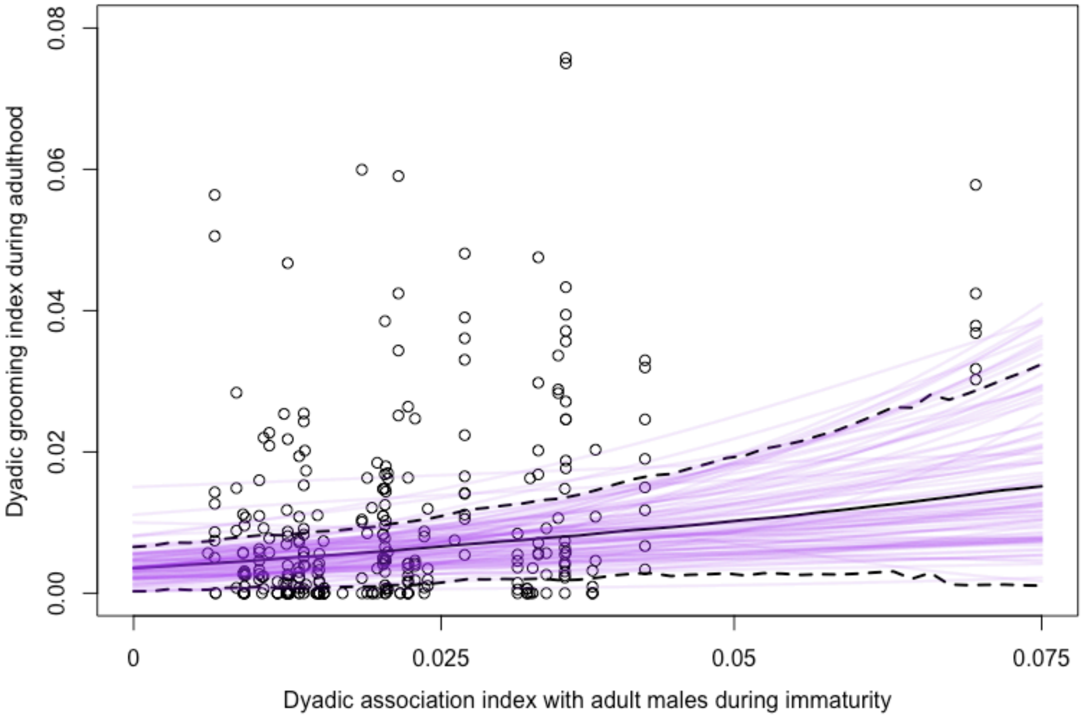
Posterior predictions for the effect of immature associations with adult males on association during adulthood



Note. Joint posterior predictions for the effect of the dyadic association index with adult males during immaturity on the dyadic association index during adulthood. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

Figure 4.4

Posterior predictions for the effect of immature associations with adult males on grooming during adulthood



Note. Joint posterior predictions for the effect of the dyadic association index with adult males during immaturity on the dyadic grooming index during adulthood. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

By contrast, I did not find an effect of early life associations among peers on their relationships as adults. Specifically, immature male dyads that had higher association indices did not have stronger association ($\beta_z = 0.06 \pm 0.30$, $\beta_g = 0.02 \pm 0.04$; Table 4.2) or grooming indices ($\beta_z = 0.00 \pm 0.32$, $\beta_g = -0.02 \pm 0.07$; Table 4.2) with those partners when they both were adults. This is evidenced by the flat relationship between the predictor and outcome variables in Figures 5 and 6, and the fact that the posterior standard deviations are larger than the posterior means.

Table 4.2

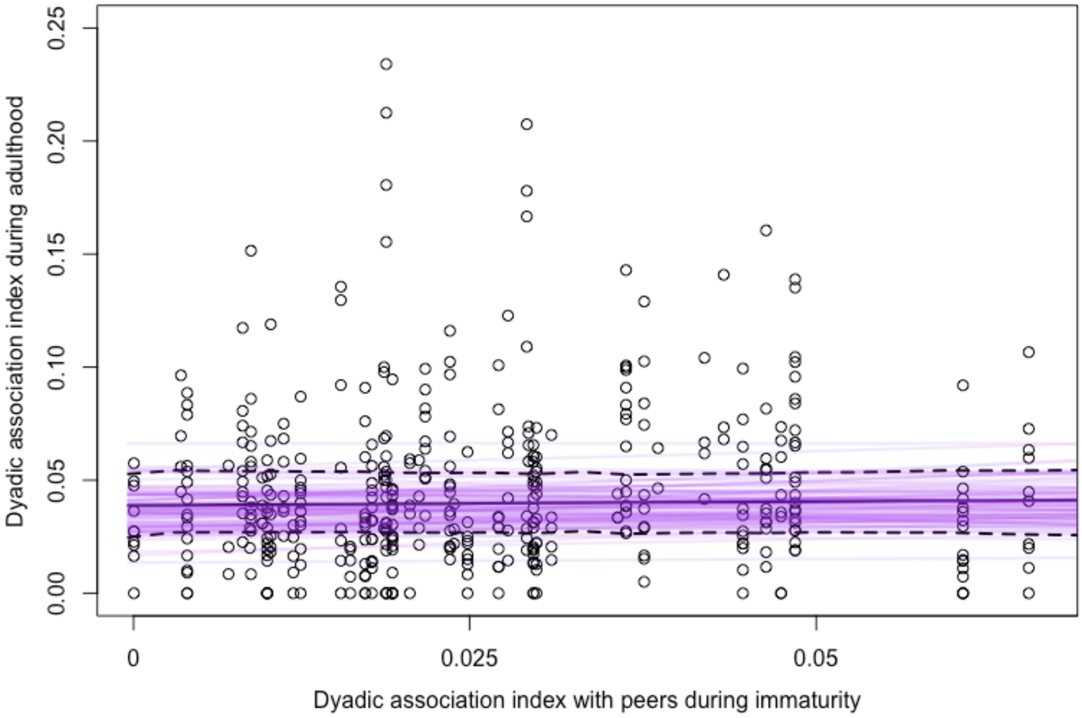
Parameter estimates for peer models

Model	Parameter	Mean	SD
Outcome: Association Predictor: Association with Male Peers while Immature	α_z Intercept	-3.51	0.92
	α_g Intercept	-3.00	0.24
	β_z Rank	-0.04	0.26
	β_g Rank	0.00	0.04
	β_z Age	0.25	0.20
	β_g Age	-0.05	0.03
	β_z Rank difference	0.01	0.30
	β_g Rank difference	0.05	0.06
	β_z Age difference	-0.40	1.05
	β_g Age difference	0.16	0.29
	β_z Association while immature	0.06	0.30
	β_g Association while immature	0.02	0.04
	β_z Joint days during target window	-0.22	0.45
	β_g Joint days during target window	0.04	0.10
	Observations (N)	*436*	
	Dyads (N)	*47*	
	Individuals (N)	*19*	
Outcome: Grooming Predictor: Association with Male Peers while Immature	α_z Intercept	-2.92	0.93
	α_g Intercept	-4.69	0.42
	β_z Rank	-0.70	0.24
	β_g Rank	0.13	0.05
	β_z Age	-0.03	0.25
	β_g Age	0.03	0.05
	β_z Rank difference	-0.10	0.26
	β_g Rank difference	-0.10	0.06
	β_z Age difference	-1.33	1.14
	β_g Age difference	0.14	0.54
	β_z Association while immature	0.00	0.32
	β_g Association while immature	-0.02	0.07
	β_z Joint days during target window	-0.52	0.46
	β_g Joint days during target window	0.17	0.19
	Observations (N)	*429*	
	Dyads (N)	*47*	
	Individuals (N)	*19*	

Note. All parameters with a subscript of z correspond with the Bernoulli component of the model, while those with a subscript of g correspond with the gamma component. Negative coefficients in the Bernoulli component indicate a lower probability of observing dyadic indices of zero, while positive values in the gamma component indicate parameters that are associated with higher dyadic indices and stronger bonds.

Figure 4.5

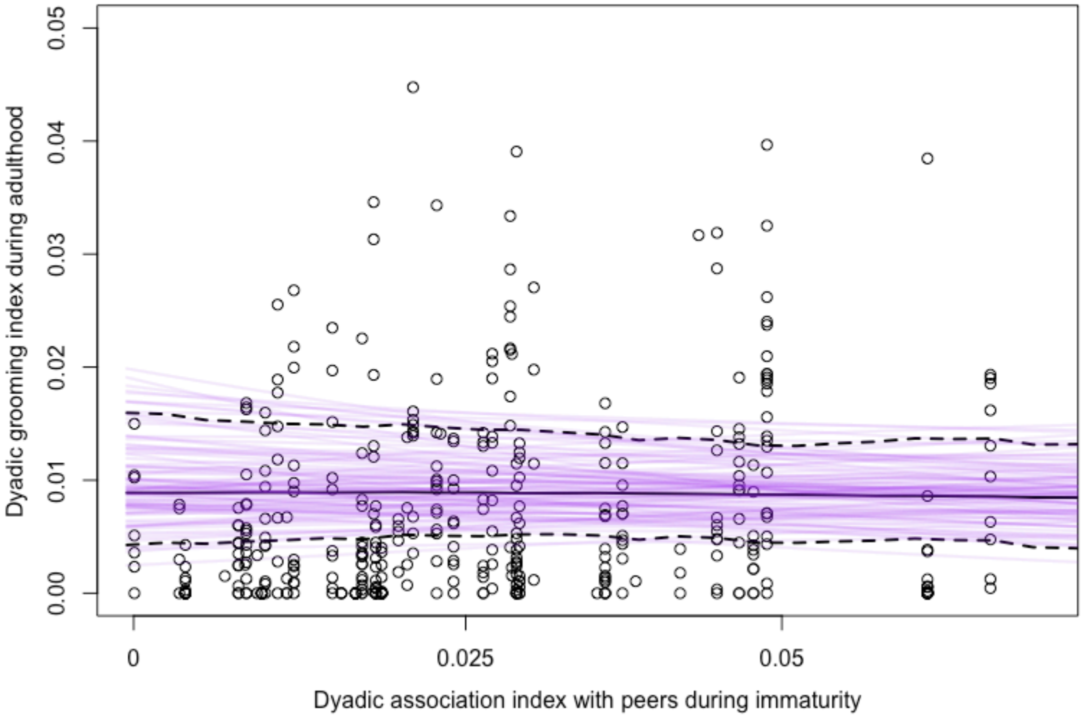
Posterior predictions for the effect of immature associations with male peers on association during adulthood



Note. Joint posterior predictions for the effect of the dyadic association index with peers during immaturity on the dyadic association index during adulthood. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

Figure 4.6

Posterior predictions for the effect of immature associations with male peers on grooming during adulthood



Note. Joint posterior predictions for the effect of the dyadic association index with peers during immaturity on the dyadic grooming index (DGI) during adulthood. Points are the raw data. Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions.

4.5 Discussion

In this study, which examined the Kasekela chimpanzee community in Gombe National Park, Tanzania, higher rates of association between immature and adult males were associated with stronger dyadic bonds between the same males in adulthood. By contrast, associations among immature peers did not persist into adulthood. This study reinforces previous studies in chimpanzees (Sandel, 2017), mountain gorillas (Rosenbaum, Hirwa, Silk, & Stoinski, 2015), and bottlenose dolphins (Gerber et al., 2020), which all found that relationships during immaturity can persist into adulthood.

What is the adaptive benefit of having early life associations with adult males persist into adulthood? In mountain gorillas, relationships that persist across developmental stages may benefit younger males in several ways, including increased mating opportunities, reduced aggression, and assistance in dominance rank competition (Rosenbaum, Hirwa, Silk, & Stoinski, 2015). In the bottlenose dolphins of Shark Bay, Australia, early life associations between males predict adult alliance partnerships (Gerber et al., 2020), which are essential for obtaining mating opportunities in adulthood (Connor et al., 2001; Connor & Krützen, 2015). Similarly, male chimpanzees face a difficult transition to adulthood (Enigk et al., 2020; Sandel, 2017), and young adult males may benefit by forming strong social bonds with older males who are past their prime by the time they reach adulthood. Although these males might not be the strongest coalition partners due to their age, older males are less aggressive (Rosati et al., 2020) and are not in direct competition with them for rank, and thus may serve as useful social partners in navigating the adult male dominance hierarchy during a difficult transition period.

In addition to direct benefits, kin selection predicts biases in behavior that raise actors' inclusive fitness (Hamilton, 1964). By preferentially associating and grooming with kin, sons and fathers could gain both direct and inclusive fitness benefits. The availability of paternity data during the study period was limited, so I was unable to conduct a comprehensive analysis of whether paternity contributed to the effects I found. Of the 6 males for whom I have paternity data, however, none had the highest rates of association with their fathers during their immature period. Nevertheless, natural selection may favor individuals to behave in ways that increase the probability of interacting with kin, and there is some evidence from Gombe that chimpanzee fathers bias their behavior toward their offspring (Murray et al., 2016). A recent study at Ngogo also found that adolescent males groom with and spend more time in close proximity to their fathers (Sandel, 2017).

What socioecological factors favor the persistence of social relationships across developmental stages? Although the social structures and mating systems of mountain gorillas, bottlenose dolphins, and chimpanzees are substantially different, all species are long-lived (Goodall, 1986; Muller & Wrangham, 2013; Robbins et al., 2001; Wells, 2014). This slow life history, combined with the challenge of entering an adult hierarchy comprised of stronger and/or more socially experienced competitors (Connor & Krützen, 2015; Enigk et al., 2020), may favor younger individuals to seek any potential advantage. Likewise, older males that are past their prime may find young adult males to be attractive partners, with the added benefit that the younger male may also be their son. Furthermore, all species that exhibit persistent relationships across developmental stages (including with maternal kin) appear to share one thing in common, which is that individuals exhibit persistent relationships with partners that represent the greatest value. These valuable partners are maternal kin in baboons and elephants (Moss et al., 2011; Silk et al., 2010a; Silk, Altmann, et al., 2006), ecologically-knowledgeable mothers in orcas (Brent et al., 2015; Foster et al., 2012), mothers in co-dominant bonobos (Surbeck et al., 2011, 2019), and adult males in the male-dominated societies of chimpanzees, bottlenose dolphins, and mountain gorillas (Goodall, 1986; Mitani, 2009b; Robbins et al., 2001; Samuels & Gifford, 1997).

There are two main limitations to the current study. First, although maternal associations are a good proxy for immature male chimpanzees' associations, they may be less useful at estimating the social interactions of immature males, so the mechanism that underlies these findings remains unresolved. For example, the persistence of social relationships with older, adult males could result from simple exposure to adult males during an immature male's formative years of development, without much social interaction, making one or both individuals more comfortable and inclined to associate when they are both adults. That being said, as immature males are more likely to be within 1 meter of adult males and to interact with them when their mothers are either nearby or grooming with adult males (Bray, unpublished data), I think a more likely scenario is that maternally mediated association is a useful proxy for rates of social interaction with adult males. The same does not apply to peers, however, who interact comfortably regardless of maternal behavior. Second, whereas older, adult males were a potential driver of association during each subject's immature and adult period, neither of the two adult males in the peer analysis were the primary drivers of their association during the immature period, which was instead mediated by their mothers. To address both limitations, future studies would benefit from a direct analysis of immature males' proximity relationships and social interactions.

Overall, these results indicate that immature male chimpanzees' associations with adult males can persist into adulthood. These findings warrant further study in other populations, as well as in other long-lived and socially complex species. Future work should also explore how maternal effects during immaturity influence other adult outcomes, such as gregariousness and rank (Wellens, 2018; Williams et al., 2002). More broadly, developmental studies can offer insight into the utility of delayed maturation, specifically how species with long developmental periods use this time to develop social skills and relationships, which are essential for survival and reproduction during adulthood.

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CHAPTER 5

CONCLUSION

In this dissertation, I found that adult males in the Kasekela chimpanzee community in Gombe National Park, Tanzania, formed strong, equitable, and enduring social bonds. Among these males, social bond strength predicted changes in dominance strength, which suggests that there are functional benefits to having strong social bonds. Lastly, immature male chimpanzees' social relationships with particular adult males, but not peers, predicted the strength of their social bonds with those same adult males when the younger males became adults.

In Chapter 2, I found that adult male chimpanzees formed strong and equitable social bonds. Not only were these bonds stable across the community for multiple years, but several bonds endured for 7 to 13 years. Maternal brothers formed stronger bonds than other dyads, and maternal brothers who were close in age or close in rank formed the strongest bonds. Among dyads that were not maternal brothers, however, the strength of social bonds was not associated with either age difference or rank difference. In addition, adult male dyads with stronger bonds groomed more equitably than dyads with weaker bonds, as did maternal brothers and dyads close in rank. These findings are consistent with previous studies from other chimpanzee communities, supporting the view that adult male social bonds are a chimpanzee universal (Watts 2000a; Langergraber et al. 2007; Gilby & Wrangham 2008; Mitani 2009a). Nevertheless, a complete understanding of male partner choice remains elusive. Demographic constraints limit the impact of kinship, and the effects of age and rank difference are small or nonexistent, suggesting that bond strength results from a more complex process than a simple accounting of basic characteristics. Instead, dyads may possess some distinct quality that engenders strength and stability, such as compatible personalities, which is associated with bond strength in captive chimpanzees, Assamese macaques, and chacma baboons (Ebenau et al., 2019; Massen & Koski, 2014; Seyfarth et al., 2014). Although personality homophily (forming social bonds with individuals of similar personality) has received relatively little attention thus far, it warrants further study.

In Chapter 3, I found that social bond strength among adult male chimpanzees predicted changes in dominance strength. These annual changes in dominance strength were themselves positively correlated with year-end changes in ordinal rank. Given that high rank generally improves male chimpanzee reproductive success (Boesch et al., 2006; Feldblum et al., under review, Inoue et al., 2008; Langergraber et al., 2013; Newton-Fisher et al., 2010; Wroblewski et al., 2009), these results indicate that the formation and maintenance of strong social bonds lead to adaptive benefits. The relationship between the strength of male social bonds and changes in dominance strength was present for sociality indices based on both associations and grooming activity, but the models with indices based on associations were more consistent and robust. Given the fission-fusion social structure of chimpanzees, both party-level associations and grooming relationships are essential components of male social bonding, and these results, in combination with prior studies, support the hypothesis that same-sex social bonds in males evolved to help individuals compete for dominance status (Ostner & Schülke, 2014). Future work should continue to refine the mechanism between sociality and fitness, while defining further the precise benefits of dominance.

In Chapter 4, I found that immature males who associated with adult males at higher rates had stronger bonds with those same adult males later in life. By contrast, rates of association between immature males were not correlated with dyadic bond strength as adults. These results reinforce previous studies in mountain gorillas (*G. beringei*) and bottlenose dolphins (*Tursiops sp.*), suggesting that the persistence of social relationships beyond those between mothers and their offspring may be more likely to evolve in long-lived species where young adult males face challenges entering an adult hierarchy comprised of stronger or more socially experienced competitors. To better understand why social relationships persist across developmental periods and address some limitations of this study, future research would benefit from detailed observation and analysis of immature males' proximity relationships and social interactions to reveal whether social exposure is sufficient or whether social interactions are necessary as well.

Together, these studies support the notion that social bonds are a chimpanzee universal, clarify the relationship between sociality and fitness, and indicate the benefits of a prolonged period of immaturity. In doing so, they aid our understanding of the evolution of cooperation (Dugatkin, 2002) and provide clues about the behavior of the last common ancestor and the evolutionary origins of human friendship (Wrangham & Pilbeam, 2002; Muller, Wrangham, & Pilbeam, 2017).

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APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Table S2.1

Parameter estimates and model diagnostics for all models

Note. Parameter estimates for all models, including posterior means and posterior standard deviations. Also included are two model diagnostics: effective sample size (ESS) and the Gelman-Rubin convergence diagnostic (Rhat).

Model	Parameter	Mean	SD	ESS	Rhat
Bond Strength Dyadic Association Index	α_z Intercept	-3.58	0.43	3694	1.00
	α_g Intercept	-3.00	0.09	4251	1.00
	β_z Rank	-0.10	0.17	5011	1.00
	β_g Rank	0.01	0.03	4889	1.00
	β_z Age	0.32	0.12	7760	1.00
	β_g Age	-0.04	0.03	4788	1.00
	β_z Maternal kinship	-2.61	1.32	7986	1.00
	β_g Maternal kinship	0.66	0.13	6865	1.00
	β_z Rank difference	-0.14	0.20	5521	1.00
	β_g Rank difference	0.09	0.03	6618	1.00
	β_z Age difference	-0.36	0.20	8868	1.00
	β_g Age difference	0.00	0.03	7304	1.00
	β_z Maternal kinship X age difference	-0.60	1.33	8198	1.00
	β_g Maternal kinship X age difference	-0.23	0.09	7243	1.00
	β_z Maternal kinship X rank difference	0.63	1.46	11064	1.00
	β_g Maternal kinship X rank difference	-0.51	0.14	7542	1.00
Bond Strength Dyadic Grooming Index	α_z Intercept	-1.87	0.47	2772	1.00
	α_g Intercept	-4.61	0.14	3753	1.00
	β_z Rank	-0.47	0.13	9486	1.00
	β_g Rank	0.12	0.04	7211	1.00
	β_z Age	-0.12	0.10	6312	1.00
	β_g Age	0.11	0.04	4233	1.00
	β_z Maternal kinship	-1.70	0.84	6629	1.00
	β_g Maternal kinship	0.38	0.20	6058	1.00
	β_z Rank difference	-0.25	0.15	9061	1.00
	β_g Rank difference	-0.06	0.04	8238	1.00
	β_z Age difference	0.19	0.15	6877	1.00
	β_g Age difference	-0.10	0.04	6579	1.00
	β_z Maternal kinship X age difference	0.74	0.52	6002	1.00

	β_g Maternal kinship X age difference	-0.13	0.14	6327	1.00
	β_z Maternal kinship X rank difference	-0.31	0.75	9458	1.00
	β_g Maternal kinship X rank difference	-0.34	0.19	9090	1.00
Grooming Equality Model with association index	α Intercept	-0.05	0.18	3557	1.00
	β Rank	0.14	0.06	7960	1.00
	β Age	0.04	0.05	7335	1.00
	β Rank difference	-0.14	0.07	8935	1.00
	β Age difference	-0.07	0.07	8074	1.00
	β Maternal kinship	0.33	0.26	7302	1.00
	β Dyadic association index	0.13	0.05	12338	1.00
	β Male community size	0.00	0.10	5539	1.00
Grooming Equality Model with grooming index	α Intercept	-0.08	0.18	3861	1.00
	β Rank	0.14	0.07	8853	1.00
	β Age	0.02	0.05	8143	1.00
	β Rank difference	-0.11	0.07	9243	1.00
	β Age difference	-0.05	0.07	10239	1.00
	β Maternal kinship	0.45	0.26	9194	1.00
	β Dyadic grooming index	0.13	0.06	12322	1.00
	β Male community size	-0.03	0.10	6370	1.00
Grooming Equality Model with no bond strength index	α Intercept	-0.03	0.18	4068	1.00
	β Rank	0.15	0.07	7557	1.00
	β Age	0.04	0.05	6819	1.00
	β Rank difference	-0.12	0.07	8846	1.00
	β Age difference	-0.07	0.07	8247	1.00
	β Maternal kinship	0.48	0.26	9212	1.00
	β Male community size	-0.04	0.10	6564	1.00
Bond Stability Dyadic Association Index (1-year Prior)	α_z Intercept	-3.56	0.36	3363	1.00
	α_g Intercept	-2.99	0.06	3180	1.00
	β_z Rank	-0.10	0.16	5328	1.00
	β_g Rank	0.01	0.03	4734	1.00
	β_z Age	0.32	0.12	7252	1.00
	β_g Age	-0.04	0.02	5198	1.00
	β_z Maternal kinship	-2.27	1.35	8622	1.00
	β_g Maternal kinship	0.25	0.12	3322	1.00
	β_z Rank difference	-0.06	0.20	5100	1.00
	β_g Rank difference	0.05	0.03	4755	1.00
	β_z Age difference	-0.57	0.22	8297	1.00
	β_g Age difference	-0.02	0.03	6787	1.00

	β_z Maternal kinship X age difference	-0.63	1.39	7909	1.00
	β_g Maternal kinship X age difference	-0.10	0.08	5728	1.00
	β_z Maternal kinship X rank difference	0.40	1.51	10914	1.00
	β_g Maternal kinship X rank difference	-0.59	0.14	7937	1.00
	β_z Prior year index	-0.51	0.23	7303	1.00
	β_g Prior year index	0.15	0.02	2695	1.00
Bond Stability Dyadic Association Index (2-years Prior)	α_z Intercept	-3.46	0.41	3513	1.00
	α_g Intercept	-2.98	0.07	4593	1.00
	β_z Rank	-0.19	0.17	5398	1.00
	β_g Rank	0.02	0.03	5209	1.00
	β_z Age	0.27	0.14	7086	1.00
	β_g Age	-0.03	0.02	6718	1.00
	β_z Maternal kinship	-2.39	1.33	10145	1.00
	β_g Maternal kinship	0.26	0.14	5026	1.00
	β_z Rank difference	-0.17	0.21	4875	1.00
	β_g Rank difference	0.08	0.04	5700	1.00
	β_z Age difference	-0.58	0.26	9001	1.00
	β_g Age difference	0.00	0.03	5485	1.00
	β_z Maternal kinship X age difference	-0.47	1.38	11129	1.00
	β_g Maternal kinship X age difference	-0.20	0.09	7935	1.00
	β_z Maternal kinship X rank difference	0.52	1.52	11407	1.00
	β_g Maternal kinship X rank difference	-0.62	0.17	8966	1.00
	β_z Prior year index	-0.01	0.19	7392	1.00
	β_g Prior year index	0.11	0.02	5026	1.00
Bond Stability Dyadic Association Index (3-years Prior)	α_z Intercept	-3.38	0.41	3411	1.00
	α_g Intercept	-3.03	0.08	4372	1.00
	β_z Rank	-0.22	0.17	6611	1.00
	β_g Rank	0.03	0.04	5241	1.00
	β_z Age	0.25	0.16	6684	1.00
	β_g Age	-0.04	0.03	5996	1.00
	β_z Maternal kinship	-2.27	1.39	10774	1.00
	β_g Maternal kinship	0.36	0.17	4630	1.00
	β_z Rank difference	-0.01	0.22	5730	1.00
	β_g Rank difference	0.10	0.04	5174	1.00
	β_z Age difference	-0.57	0.28	7872	1.00
	β_g Age difference	0.00	0.04	5606	1.00
	β_z Maternal kinship X age difference	-0.44	1.43	10593	1.00
	β_g Maternal kinship X age difference	-0.25	0.12	5962	1.00

	β_z Maternal kinship X rank difference	0.36	1.50	11386	1.00
	β_g Maternal kinship X rank difference	-0.75	0.20	7472	1.00
	β_z Prior year index	-0.22	0.20	9646	1.00
	β_g Prior year index	0.01	0.03	4517	1.00
Bond Stability Dyadic Association Index (4-years Prior)	α_z Intercept	-3.17	0.44	4073	1.00
	α_g Intercept	-3.05	0.07	6194	1.00
	β_z Rank	-0.23	0.19	6766	1.00
	β_g Rank	0.02	0.04	5589	1.00
	β_z Age	0.20	0.17	7726	1.00
	β_g Age	-0.05	0.03	8021	1.00
	β_z Maternal kinship	-2.25	1.39	10147	1.00
	β_g Maternal kinship	0.28	0.17	7297	1.00
	β_z Rank difference	-0.03	0.24	6436	1.00
	β_g Rank difference	0.08	0.05	5856	1.00
	β_z Age difference	-0.49	0.31	9232	1.00
	β_g Age difference	0.06	0.05	6885	1.00
	β_z Maternal kinship X age difference	-0.32	1.53	11767	1.00
	β_g Maternal kinship X age difference	-0.24	0.13	7386	1.00
	β_z Maternal kinship X rank difference	0.54	1.50	13066	1.00
	β_g Maternal kinship X rank difference	-0.64	0.22	7956	1.00
	β_z Prior year index	-0.02	0.19	7397	1.00
	β_g Prior year index	0.00	0.03	7343	1.00
Bond Stability Dyadic Association Index (5-years Prior)	α_z Intercept	-3.46	0.59	3131	1.00
	α_g Intercept	-3.01	0.08	4002	1.00
	β_z Rank	-0.27	0.22	4771	1.00
	β_g Rank	0.03	0.04	4200	1.00
	β_z Age	0.14	0.21	5198	1.00
	β_g Age	-0.06	0.04	4383	1.00
	β_z Maternal kinship	-2.07	1.50	8375	1.00
	β_g Maternal kinship	0.25	0.18	5145	1.00
	β_z Rank difference	-0.12	0.29	4702	1.00
	β_g Rank difference	0.08	0.06	4454	1.00
	β_z Age difference	-0.51	0.41	4276	1.00
	β_g Age difference	0.10	0.06	4218	1.00
	β_z Maternal kinship X age difference	-0.31	1.54	8360	1.00
	β_g Maternal kinship X age difference	-0.24	0.15	5294	1.00
	β_z Maternal kinship X rank difference	0.55	1.56	8727	1.00
	β_g Maternal kinship X rank difference	-0.73	0.25	5564	1.00

	β_z Prior year index	0.17	0.20	6764	1.00
	β_g Prior year index	-0.03	0.03	5672	1.00
Bond Stability Dyadic Grooming Index (1-year Prior)	α_z Intercept	-2.10	0.49	3980	1.00
	α_g Intercept	-4.56	0.16	3789	1.00
	β_z Rank	-0.57	0.15	8327	1.00
	β_g Rank	0.13	0.04	6944	1.00
	β_z Age	-0.02	0.12	7420	1.00
	β_g Age	0.10	0.05	4253	1.00
	β_z Maternal kinship	-1.50	0.94	6641	1.00
	β_g Maternal kinship	0.39	0.23	6760	1.00
	β_z Rank difference	-0.22	0.17	9295	1.00
	β_g Rank difference	-0.04	0.05	8191	1.00
	β_z Age difference	0.16	0.19	7191	1.00
	β_g Age difference	-0.09	0.05	7643	1.00
	β_z Maternal kinship X age difference	0.77	0.57	6885	1.00
	β_g Maternal kinship X age difference	-0.20	0.15	6921	1.00
	β_z Maternal kinship X rank difference	-0.46	0.84	8699	1.00
	β_g Maternal kinship X rank difference	-0.39	0.21	8833	1.00
	β_z Prior year index	-0.39	0.23	7564	1.00
	β_g Prior year index	-0.02	0.03	5785	1.00
Bond Stability Dyadic Grooming Index (2-years Prior)	α_z Intercept	-2.14	0.57	4494	1.00
	α_g Intercept	-4.56	0.16	5910	1.00
	β_z Rank	-0.58	0.18	10580	1.00
	β_g Rank	0.12	0.05	9513	1.00
	β_z Age	0.09	0.13	10850	1.00
	β_g Age	0.06	0.05	5806	1.00
	β_z Maternal kinship	-1.15	1.01	8938	1.00
	β_g Maternal kinship	0.24	0.24	7883	1.00
	β_z Rank difference	-0.32	0.20	11136	1.00
	β_g Rank difference	-0.04	0.05	9346	1.00
	β_z Age difference	0.01	0.23	9450	1.00
	β_g Age difference	-0.06	0.06	9593	1.00
	β_z Maternal kinship X age difference	0.74	0.64	8214	1.00
	β_g Maternal kinship X age difference	-0.17	0.15	8334	1.00
	β_z Maternal kinship X rank difference	-0.34	0.91	13492	1.00
	β_g Maternal kinship X rank difference	-0.42	0.23	11717	1.00
	β_z Prior year index	-0.35	0.24	9794	1.00
	β_g Prior year index	0.02	0.03	7886	1.00

Bond Stability Dyadic Grooming Index (3-years Prior)	α_z Intercept	-2.24	0.63	3878	1.00
	α_g Intercept	-4.59	0.15	4522	1.00
	β_z Rank	-0.61	0.20	9074	1.00
	β_g Rank	0.10	0.05	8886	1.00
	β_z Age	0.06	0.15	8673	1.00
	β_g Age	0.07	0.06	5530	1.00
	β_z Maternal kinship	-0.51	1.00	10242	1.00
	β_g Maternal kinship	0.02	0.22	8652	1.00
	β_z Rank difference	-0.29	0.23	8680	1.00
	β_g Rank difference	-0.01	0.06	7797	1.00
	β_z Age difference	0.03	0.27	8307	1.00
	β_g Age difference	-0.04	0.05	9863	1.00
	β_z Maternal kinship X age difference	0.38	0.70	9188	1.00
	β_g Maternal kinship X age difference	-0.11	0.14	8797	1.00
	β_z Maternal kinship X rank difference	-0.41	0.96	10870	1.00
	β_g Maternal kinship X rank difference	-0.37	0.25	11582	1.00
	β_z Prior year index	-0.41	0.25	11607	1.00
	β_g Prior year index	0.12	0.03	6010	1.00
Bond Stability Dyadic Grooming Index (4-years Prior)	α_z Intercept	-2.52	0.71	5711	1.00
	α_g Intercept	-4.54	0.19	6436	1.00
	β_z Rank	-0.61	0.22	9206	1.00
	β_g Rank	0.10	0.06	10679	1.00
	β_z Age	0.15	0.17	11698	1.00
	β_g Age	0.10	0.07	7538	1.00
	β_z Maternal kinship	0.03	1.08	13893	1.00
	β_g Maternal kinship	0.17	0.27	10317	1.00
	β_z Rank difference	-0.27	0.26	8509	1.00
	β_g Rank difference	0.07	0.06	10019	1.00
	β_z Age difference	0.04	0.33	11186	1.00
	β_g Age difference	-0.04	0.07	9654	1.00
	β_z Maternal kinship X age difference	0.68	0.76	10852	1.00
	β_g Maternal kinship X age difference	-0.12	0.19	10851	1.00
	β_z Maternal kinship X rank difference	-0.17	1.01	13680	1.00
	β_g Maternal kinship X rank difference	-0.28	0.27	13421	1.00
	β_z Prior year index	0.19	0.21	9520	1.00
	β_g Prior year index	0.00	0.04	9115	1.00
	α_z Intercept	-2.30	0.55	2787	1.00
	α_g Intercept	-4.41	0.19	2601	1.00

Bond Stability Dyadic Grooming Index (5-years Prior)	β_z Rank	-0.83	0.23	3110	1.00
	β_g Rank	0.09	0.06	3724	1.00
	β_z Age	0.11	0.19	4514	1.00
	β_g Age	0.02	0.07	3311	1.00
	β_z Maternal kinship	0.05	1.13	4913	1.00
	β_g Maternal kinship	0.03	0.29	4121	1.00
	β_z Rank difference	-0.02	0.27	2802	1.00
	β_g Rank difference	0.04	0.07	3904	1.00
	β_z Age difference	-0.02	0.35	4576	1.00
	β_g Age difference	0.01	0.08	4137	1.00
	β_z Maternal kinship X age difference	-0.48	1.03	4833	1.00
	β_g Maternal kinship X age difference	-0.18	0.21	4802	1.00
	β_z Maternal kinship X rank difference	-1.46	1.11	5371	1.00
	β_g Maternal kinship X rank difference	-0.11	0.30	5204	1.00
	β_z Prior year index	-0.66	0.31	7044	1.00
	β_g Prior year index	0.11	0.04	4521	1.00

APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Table S3.1

Parameter estimates and model diagnostics for all models

Note. Parameter estimates for all models, including posterior means and standard deviations. Also included are two model diagnostics: effective sample size (ESS) and the Gelman-Rubin convergence diagnostic (Rhat).

Model Set	Key	Index	Parameter	Mean	SD	ESS	Rhat
Party-level associations (dyadic strength)	A1	Sum of all dyadic indices	Intercept	0.07	0.09	4125	1.00
			Age	-0.22	0.07	5958	1.00
			Mean Elo score (dominance)	-0.44	0.11	3603	1.00
			Sociality index	0.21	0.06	7680	1.00
			Dominance X Age	-0.28	0.10	4758	1.00
			Dominance X Sociality index	0.05	0.06	6855	1.00
	A2	Mean of all dyadic indices	Intercept	0.05	0.09	3126	1.00
			Age	-0.22	0.07	4764	1.00
			Mean Elo score (dominance)	-0.45	0.11	2808	1.00
			Sociality index	0.18	0.07	5116	1.00
			Dominance X Age	-0.28	0.11	4317	1.00
			Dominance X Sociality index	0.05	0.06	5028	1.00
	A3	Sum of dyadic indices that are above the mean	Intercept	0.07	0.09	3768	1.00
			Age	-0.23	0.07	5379	1.00
			Mean Elo score (dominance)	-0.45	0.11	2987	1.00
			Sociality index	0.24	0.06	6491	1.00
			Dominance X Age	-0.28	0.11	3836	1.00
			Dominance X Sociality index	0.05	0.06	4986	1.00
	A4	Sum of dyadic indices that are ≥ 1 SD above the mean	Intercept	0.05	0.09	5013	1.00
			Age	-0.24	0.07	5717	1.00
			Mean Elo score (dominance)	-0.44	0.11	3437	1.00
			Sociality index	0.12	0.07	8829	1.00
			Dominance X Age	-0.29	0.11	4390	1.00
			Dominance X Sociality index	0.04	0.06	8487	1.00
	A5	Number of dyadic indices that are above the mean	Intercept	-0.39	0.13	4456	1.00
			Age	-0.24	0.07	4343	1.00
			Mean Elo score (dominance)	-0.44	0.16	1917	1.00
			Sociality index	0.16	0.04	4214	1.00
			Dominance X Age	-0.28	0.10	4077	1.00
			Dominance X Sociality index	0.01	0.04	3139	1.00
	A6	Number of dyadic indices that are ≥ 1 SD above the mean	Intercept	-0.07	0.11	4547	1.00
			Age	-0.24	0.07	5646	1.00
			Mean Elo score (dominance)	-0.39	0.13	2870	1.00
			Sociality index	0.12	0.06	5665	1.00
			Dominance X Age	-0.28	0.11	4754	1.00
			Dominance X Sociality index	-0.01	0.05	5026	1.00
Party-level associations	A7	Proportion of arrivals with adult males	Intercept	0.05	0.09	2721	1.00
			Age	-0.25	0.07	5193	1.00
			Mean Elo score (dominance)	-0.41	0.11	2941	1.00
			Sociality index	0.16	0.07	5463	1.00

(overall sociality)			Dominance X Age	-0.27	0.11	3930	1.00
			Dominance X Sociality index	0.07	0.07	6607	1.00
	A8	Mean number of adult males in each arrival	Intercept	0.08	0.09	4412	1.00
			Age	-0.27	0.07	4853	1.00
			Mean Elo score (dominance)	-0.33	0.11	4055	1.00
			Sociality index	0.10	0.07	6298	1.00
			Dominance X Age	-0.27	0.11	4642	1.00
			Dominance X Sociality index	0.13	0.07	7945	1.00
Grooming (dyadic strength, controlling for time together)	G1	Sum of all dyadic indices	Intercept	0.03	0.08	4437	1.00
			Age	-0.24	0.07	3347	1.00
			Mean Elo score (dominance)	-0.38	0.10	2560	1.00
			Sociality index	0.04	0.12	3088	1.00
			Dominance X Age	-0.23	0.10	3769	1.00
			Dominance X Sociality index	0.15	0.10	4524	1.00
	G2	Mean of all dyadic indices	Intercept	0.04	0.08	4763	1.00
			Age	-0.26	0.08	3559	1.00
			Mean Elo score (dominance)	-0.40	0.10	2833	1.00
			Sociality index	0.06	0.15	3335	1.00
			Dominance X Age	-0.24	0.10	3544	1.00
			Dominance X Sociality index	0.17	0.11	4353	1.00
	G3	Sum of dyadic indices that are above the mean	Intercept	0.03	0.08	3672	1.00
			Age	-0.24	0.07	3458	1.00
			Mean Elo score (dominance)	-0.38	0.10	2847	1.00
			Sociality index	0.03	0.12	3229	1.00
			Dominance X Age	-0.24	0.10	3756	1.00
			Dominance X Sociality index	0.16	0.09	4574	1.00
	G4	Sum of dyadic indices that are ≥ 1 SD above the mean	Intercept	0.04	0.07	3600	1.00
			Age	-0.24	0.07	3463	1.00
			Mean Elo score (dominance)	-0.37	0.10	2042	1.00
			Sociality index	-0.03	0.09	3373	1.00
			Dominance X Age	-0.26	0.11	2936	1.00
			Dominance X Sociality index	0.05	0.08	5059	1.00
	G5	Number of dyadic indices that are above the mean	Intercept	0.06	0.13	4080	1.00
			Age	-0.24	0.07	4908	1.00
			Mean Elo score (dominance)	-0.47	0.16	3714	1.00
			Sociality index	0.00	0.04	4137	1.00
			Dominance X Age	-0.29	0.11	4781	1.00
			Dominance X Sociality index	0.02	0.04	4621	1.00
	G6	Number of dyadic indices that are ≥ 1 SD above the mean	Intercept	0.10	0.09	4860	1.00
			Age	-0.24	0.07	4464	1.00
			Mean Elo score (dominance)	-0.42	0.12	3902	1.00
			Sociality index	-0.03	0.07	3756	1.00
			Dominance X Age	-0.30	0.10	4699	1.00
			Dominance X Sociality index	0.02	0.06	4560	1.00
Grooming (dyadic strength, controlling for observation time)	G7	Sum of all dyadic indices	Intercept	-0.01	0.09	2901	1.00
			Age	-0.27	0.08	3265	1.00
			Mean Elo score (dominance)	-0.50	0.11	2376	1.00
			Sociality index	0.15	0.09	3677	1.00
			Dominance X Age	-0.28	0.11	2327	1.00
			Dominance X Sociality index	0.16	0.07	4602	1.00
	G8		Intercept	0.00	0.09	3860	1.00
			Age	-0.28	0.09	3098	1.00

		Mean of all dyadic indices	Mean Elo score (dominance)	-0.48	0.11	2596	1.00
			Sociality index	0.16	0.11	2822	1.00
			Dominance X Age	-0.28	0.11	2825	1.00
			Dominance X Sociality index	0.17	0.08	4043	1.00
	G9	Sum of dyadic indices that are above the mean	Intercept	0.00	0.09	3917	1.00
			Age	-0.28	0.09	3898	1.00
			Mean Elo score (dominance)	-0.50	0.11	3004	1.00
			Sociality index	0.18	0.08	4015	1.00
			Dominance X Age	-0.27	0.11	2980	1.00
			Dominance X Sociality index	0.14	0.07	4558	1.00
	G10	Sum of dyadic indices that are ≥ 1 SD above the mean	Intercept	0.02	0.09	4317	1.00
			Age	-0.27	0.08	4407	1.00
			Mean Elo score (dominance)	-0.48	0.11	2754	1.00
			Sociality index	0.15	0.08	4141	1.00
			Dominance X Age	-0.27	0.11	3896	1.00
			Dominance X Sociality index	0.10	0.07	6779	1.00
	G11	Number of dyadic indices that are above the mean	Intercept	-0.18	0.14	3316	1.00
			Age	-0.28	0.08	3783	1.00
			Mean Elo score (dominance)	-0.61	0.17	3083	1.00
			Sociality index	0.09	0.05	3237	1.00
			Dominance X Age	-0.28	0.11	4940	1.00
			Dominance X Sociality index	0.05	0.04	3980	1.00
	G12	Number of dyadic indices that are ≥ 1 SD above the mean	Intercept	0.10	0.09	4860	1.00
			Age	-0.24	0.07	4464	1.00
			Mean Elo score (dominance)	-0.42	0.12	3902	1.00
			Sociality index	-0.03	0.07	3756	1.00
			Dominance X Age	-0.30	0.10	4699	1.00
			Dominance X Sociality index	0.02	0.06	4560	1.00
Grooming (overall sociality)	G13	Proportion of time grooming with adult males (total)	Intercept	0.01	0.08	4718	1.00
			Age	-0.29	0.08	4245	1.00
			Mean Elo score (dominance)	-0.42	0.11	3004	1.00
			Sociality index	0.16	0.08	6818	1.00
			Dominance X Age	-0.24	0.11	4264	1.00
			Dominance X Sociality index	0.00	0.09	6267	1.00
	G14	Proportion of time grooming with adult males (mutual)	Intercept	0.02	0.08	3359	1.00
			Age	-0.29	0.08	2879	1.00
			Mean Elo score (dominance)	-0.39	0.11	1969	1.00
			Sociality index	0.13	0.08	4137	1.00
			Dominance X Age	-0.24	0.11	2466	1.00
			Dominance X Sociality index	-0.05	0.08	5340	1.00
	G15	Proportion of time grooming with adult males (give)	Intercept	0.02	0.08	3933	1.00
			Age	-0.28	0.07	3320	1.00
			Mean Elo score (dominance)	-0.39	0.10	2308	1.00
			Sociality index	0.14	0.08	4789	1.00
			Dominance X Age	-0.24	0.10	2997	1.00
			Dominance X Sociality index	-0.06	0.08	6556	1.00
	G16	Proportion of time grooming with adult males (receive)	Intercept	0.00	0.08	3299	1.00
			Age	-0.28	0.08	3179	1.00
			Mean Elo score (dominance)	-0.43	0.10	2364	1.00
			Sociality index	0.15	0.08	4333	1.00
			Dominance X Age	-0.25	0.11	2905	1.00
			Dominance X Sociality index	0.06	0.09	4627	1.00

Table S3.2

Descriptive statistics for the Kasekela chimpanzee community

Year	# of adult males in community	Mean # of joint first arrivals per male-male dyad	Mean minutes spent in the same party while one member is focal per male-male	Mean # of minutes spent grooming per male-male dyad	Mean party size per adult male	Mean adult male party size per adult male	Observed pant grunts among adult males
1979	5	16.0	6249	227.5	3.5	2.3	79
1980	6	16.1	6785	168.3	3.7	2.6	33
1981	6	9.9	3278	86.0	3.9	2.6	11
1982	5	9.4	3934	88.5	3.9	2.1	41
1983	6	8.7	7446	174.7	5.3	2.9	79
1984	6	5.9	6534	201.7	6.2	3.4	92
1985	7	4.2	7116	116.3	5.7	3.4	104
1986	7	6.0	2919	181.7	3.2	2.1	157
1987	6	8.4	8977	91.7	5.6	3.3	331
1988	7	6.1	12941	132.1	6.6	4.0	403
1989	7	6.5	8104	127.1	5.4	3.4	236
1990	7	4.4	14767	178.1	9.1	4.8	77
1991	7	6.3	19276	219.5	7.6	5.0	108
1992	8	10.8	10517	106.8	5.5	3.9	149
1993	9	4.9	14509	105.7	9.3	6.8	62
1994	9	4.2	13700	88.1	9.1	6.6	87
1995	10	4.5	11544	104.2	8.8	6.5	154
1996	10	5.4	10627	74.4	7.9	6.0	193
1997	10	4.3	10877	58.6	9.6	6.8	112
1998	10	4.2	9708	69.2	8.2	5.8	163
1999	9	2.0	8986	39.6	10.4	6.8	86
2000	10	3.4	5765	54.3	9.2	6.0	95
2001	10	3.6	8113	56.6	10.2	6.5	89
2002	9	4.6	8027	73.8	7.7	5.1	105
2003	9	3.1	8580	99.5	7.9	4.5	32
2004	8	3.6	7558	77.1	8.7	4.7	30
2005	8	3.6	7625	49.9	10.3	5.8	5
2006	8	2.9	6162	54.9	11.9	6.4	43
2007	8	3.1	8744	61.2	11.6	6.2	45
2008	7	3.3	7024	53.6	14.9	7.0	27
2009	5	2.4	5133	27.6	13.1	7.4	23
2010	9	3.5	4306	29.5	12.2	6.9	56
2011	9	4.1	2541	48.7	7.3	4.1	63
2012	11	3.4	4251	32.6	10.9	5.8	145
2013	8	3.7	4123	38.6	9.9	4.1	150
2014	7	5.2	7055	93.3	11.3	4.2	230

Figure S3.1

Correlation matrix of all sociality indices based on party-level associations

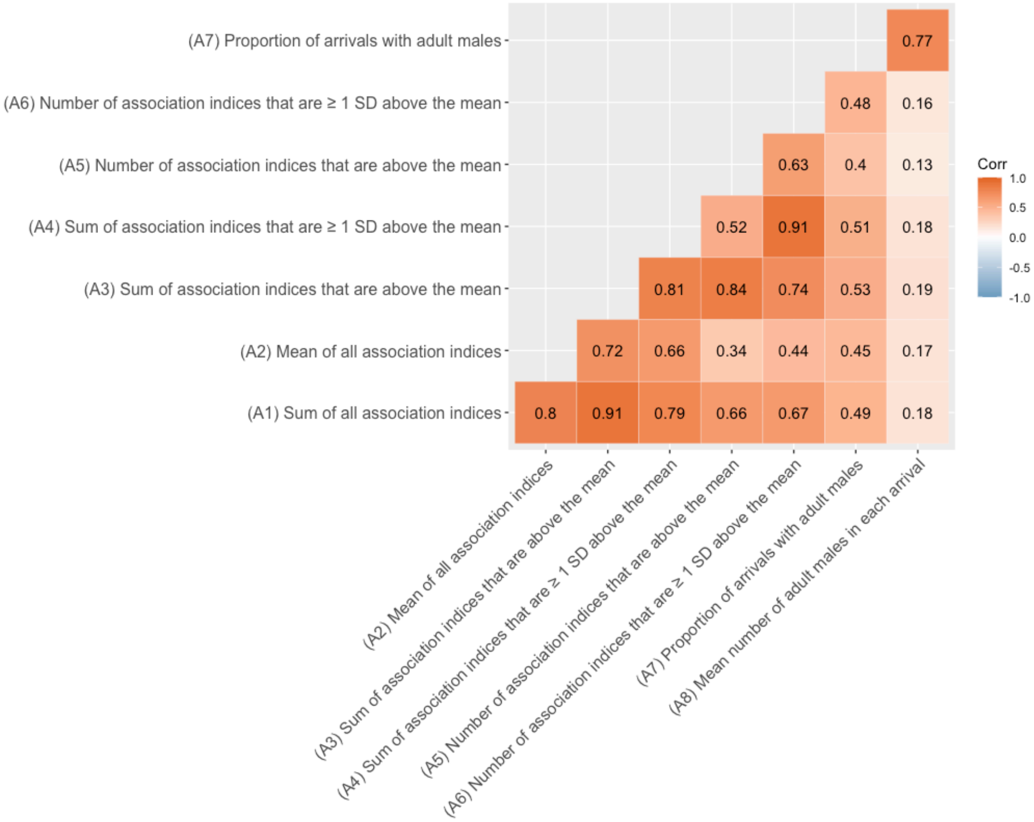
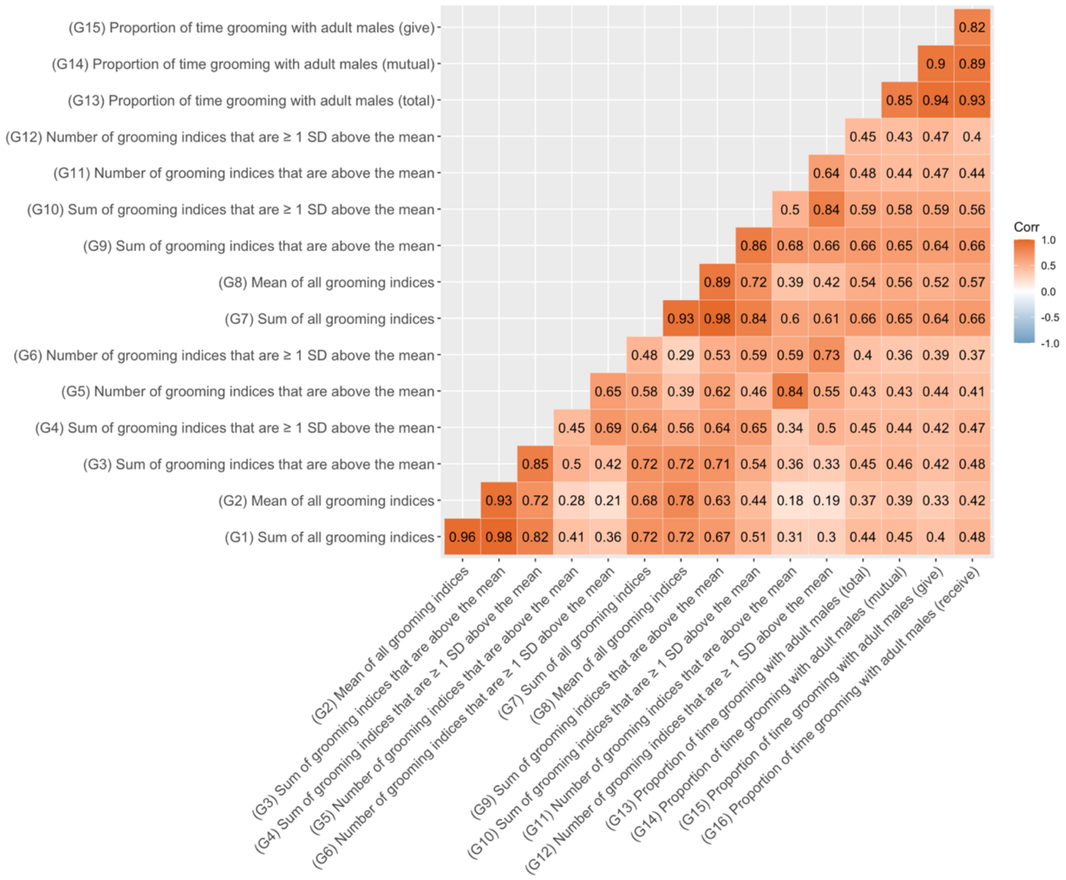


Figure S3.2

Correlation matrix of all sociality indices based on grooming activity



	(G2) Mean of all grooming indices	(G3) Sum of grooming indices that are above the mean	(G4) Sum of grooming indices that are ≥ 1 SD above the mean	(G5) Number of grooming indices that are above the mean	(G6) Number of grooming indices that are ≥ 1 SD above the mean	(G7) Sum of all grooming indices	(G8) Mean of all grooming indices	(G9) Sum of grooming indices that are above the mean	(G10) Sum of grooming indices that are ≥ 1 SD above the mean	(G11) Number of grooming indices that are above the mean	(G12) Number of grooming indices that are ≥ 1 SD above the mean	(G13) Proportion of time grooming with adult males (total)	(G14) Proportion of time grooming with adult males (mutual)	(G15) Proportion of time grooming with adult males (give)	(G16) Proportion of time grooming with adult males (receive)
(G15) Proportion of time grooming with adult males (give)															0.82
(G14) Proportion of time grooming with adult males (mutual)														0.9	0.89
(G13) Proportion of time grooming with adult males (total)													0.85	0.94	0.93
(G12) Number of grooming indices that are ≥ 1 SD above the mean												0.45	0.43	0.47	0.4
(G11) Number of grooming indices that are above the mean											0.64	0.48	0.44	0.47	0.44
(G10) Sum of grooming indices that are ≥ 1 SD above the mean										0.5	0.84	0.59	0.58	0.59	0.56
(G9) Sum of grooming indices that are above the mean									0.86	0.68	0.66	0.66	0.65	0.64	0.66
(G8) Mean of all grooming indices								0.89	0.72	0.39	0.42	0.54	0.56	0.52	0.57
(G7) Sum of all grooming indices							0.93	0.98	0.84	0.6	0.61	0.66	0.65	0.64	0.66
(G6) Number of grooming indices that are ≥ 1 SD above the mean						0.48	0.29	0.53	0.59	0.59	0.73	0.4	0.36	0.39	0.37
(G5) Number of grooming indices that are above the mean					0.65	0.58	0.39	0.62	0.46	0.84	0.55	0.43	0.43	0.44	0.41
(G4) Sum of grooming indices that are ≥ 1 SD above the mean				0.45	0.69	0.64	0.56	0.64	0.65	0.34	0.5	0.45	0.44	0.42	0.47
(G3) Sum of grooming indices that are above the mean			0.85	0.5	0.42	0.72	0.72	0.71	0.54	0.36	0.33	0.45	0.46	0.42	0.48
(G2) Mean of all grooming indices		0.93	0.72	0.28	0.21	0.68	0.78	0.63	0.44	0.18	0.19	0.37	0.39	0.33	0.42
(G1) Sum of all grooming indices	0.96	0.98	0.82	0.41	0.36	0.72	0.72	0.67	0.51	0.31	0.3	0.44	0.45	0.4	0.48

Figure S3.3

Distribution of all annual dyadic association indices

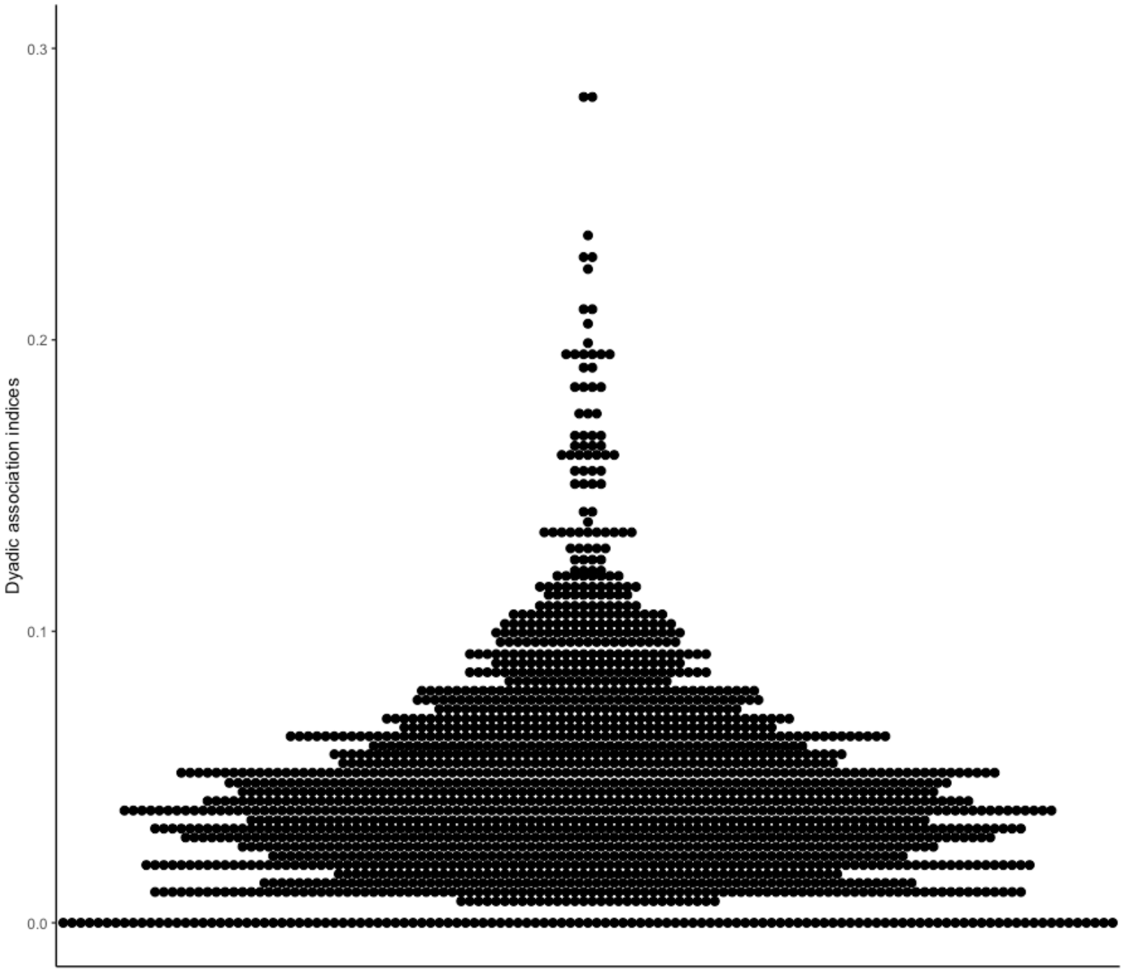


Figure S3.4

Distribution of all annual dyadic grooming indices

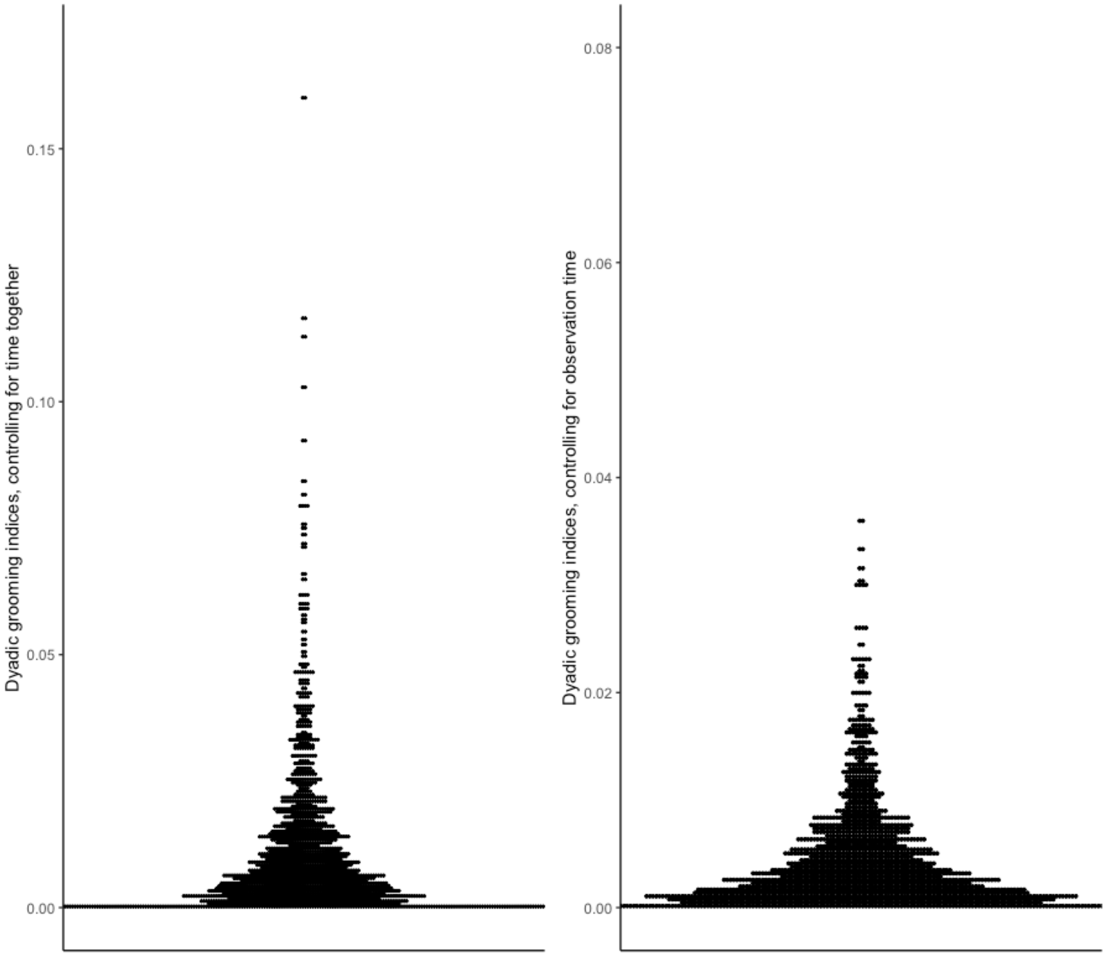
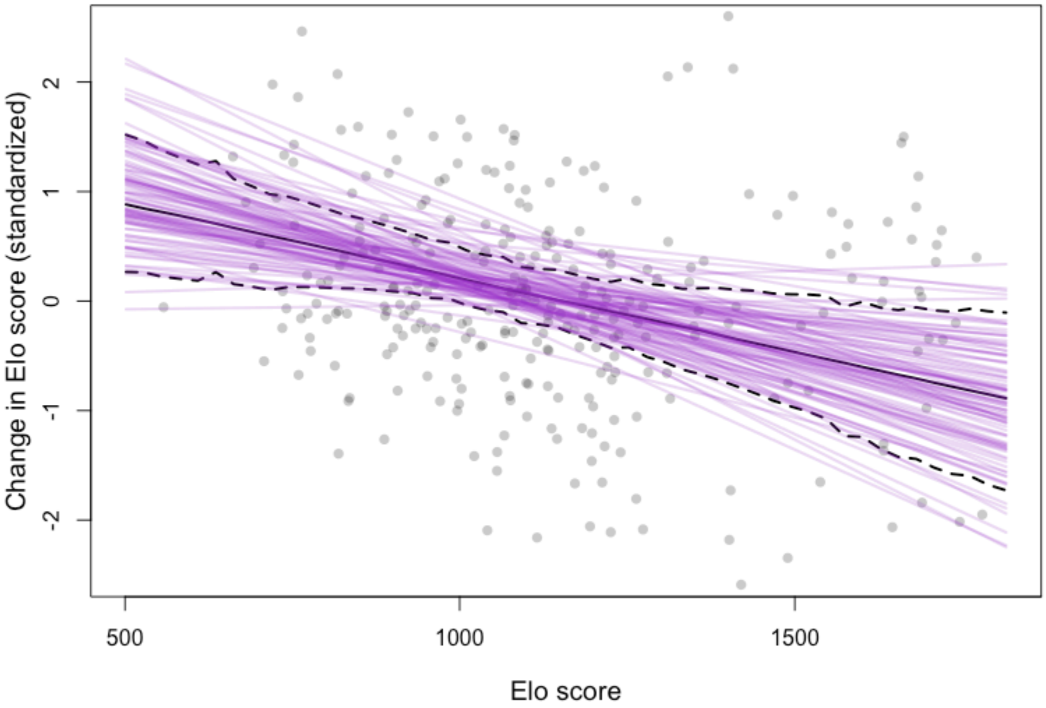


Figure S3.5

Posterior predictions for the influence of Elo score on subsequent change in Elo score



Note. Posterior predictions for the influence of Elo score on subsequent change in Elo score for all adult males. Model predictions were based on the best-fit association model (A5). Solid black lines represent median estimates; dashed lines indicate 89% credible intervals. Purple lines are 100 randomly drawn posterior predictions. Grey dots are raw data.

Figure S3.6

Male Elo scores (≥ 15 years old) from 1979-1988

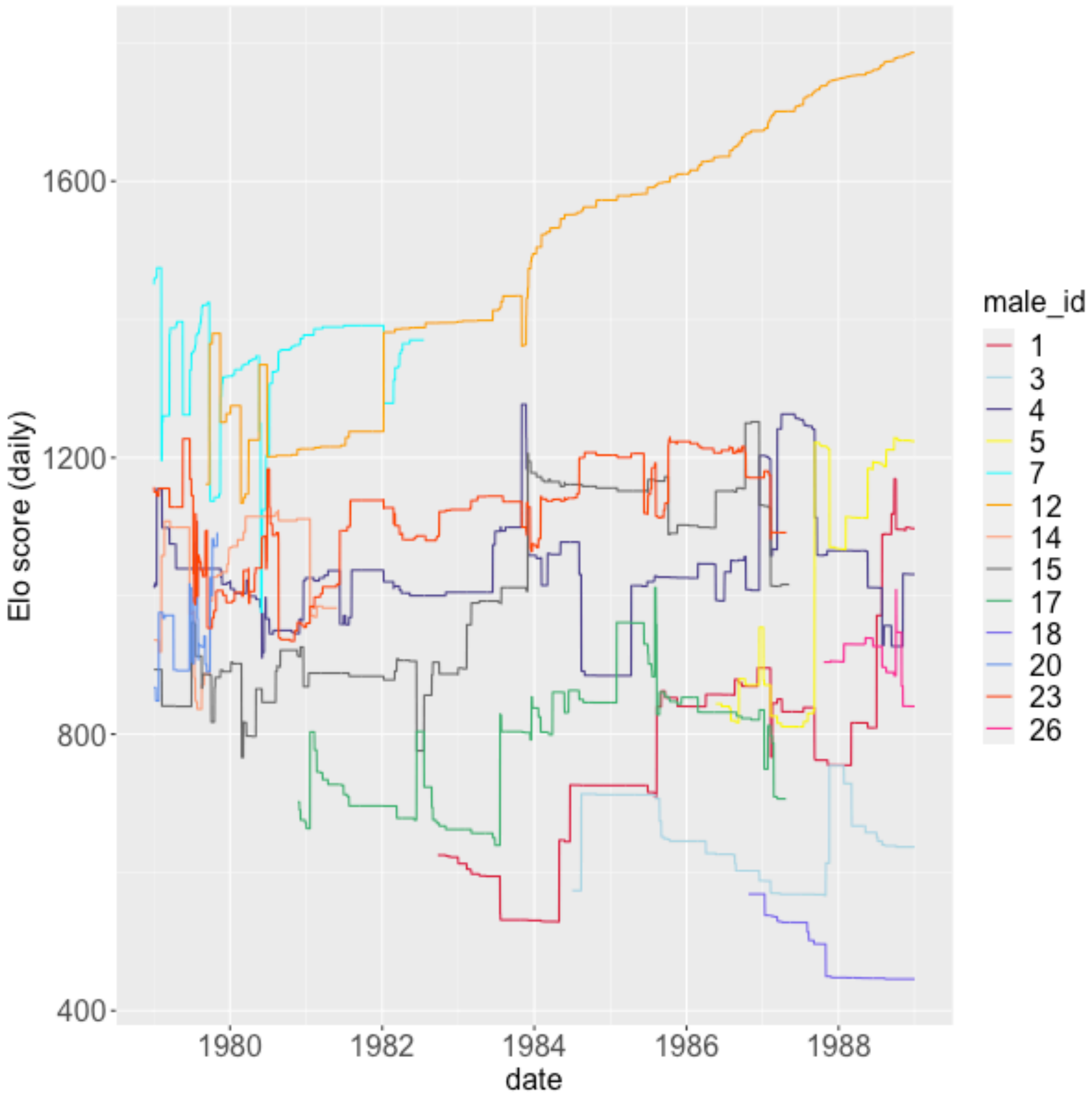


Figure S3.7

Male Elo scores (≥ 15 years old) from 1989-1997

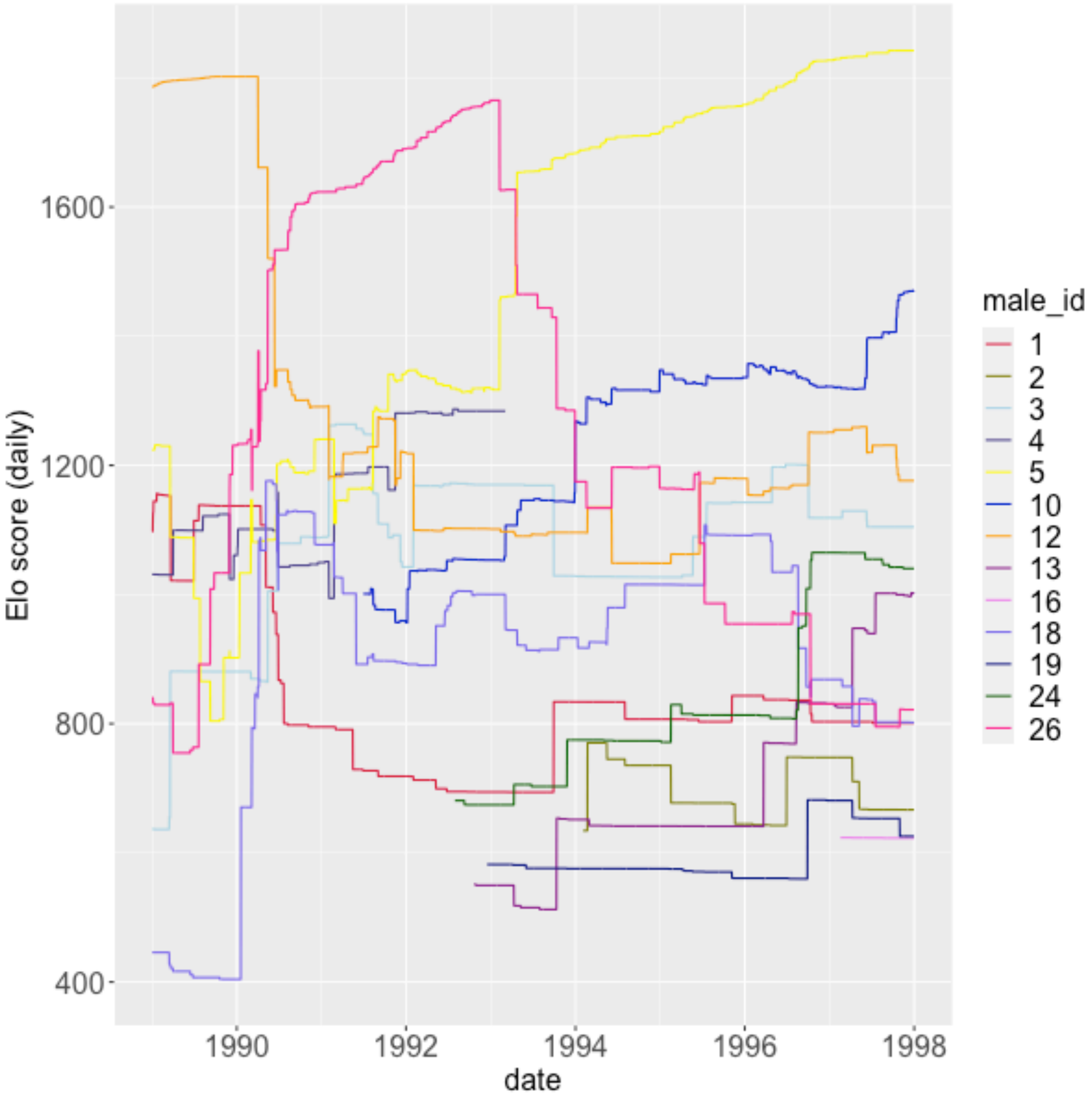


Figure S3.8

Male Elo scores (≥ 15 years old) from 1998-2006

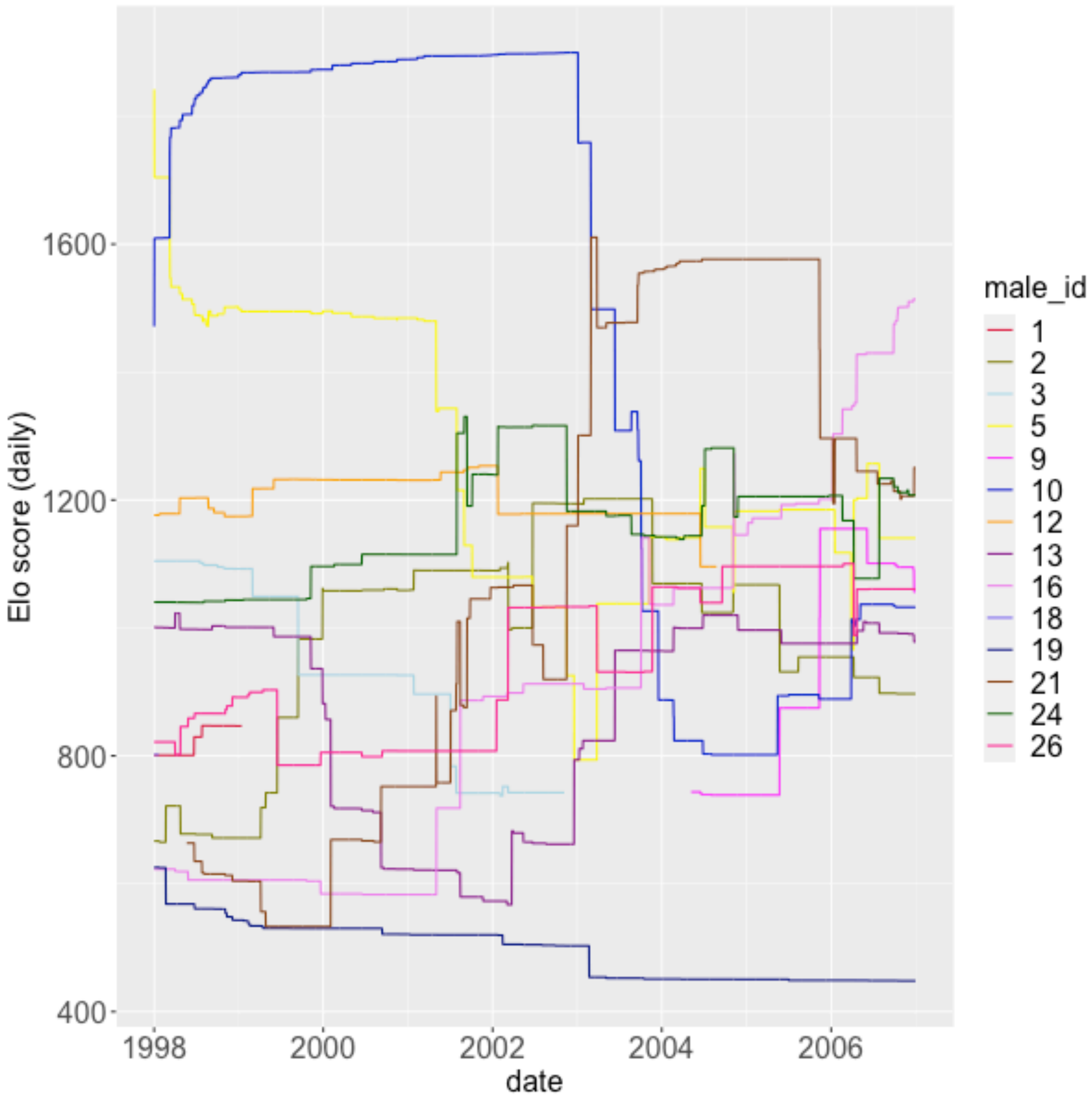
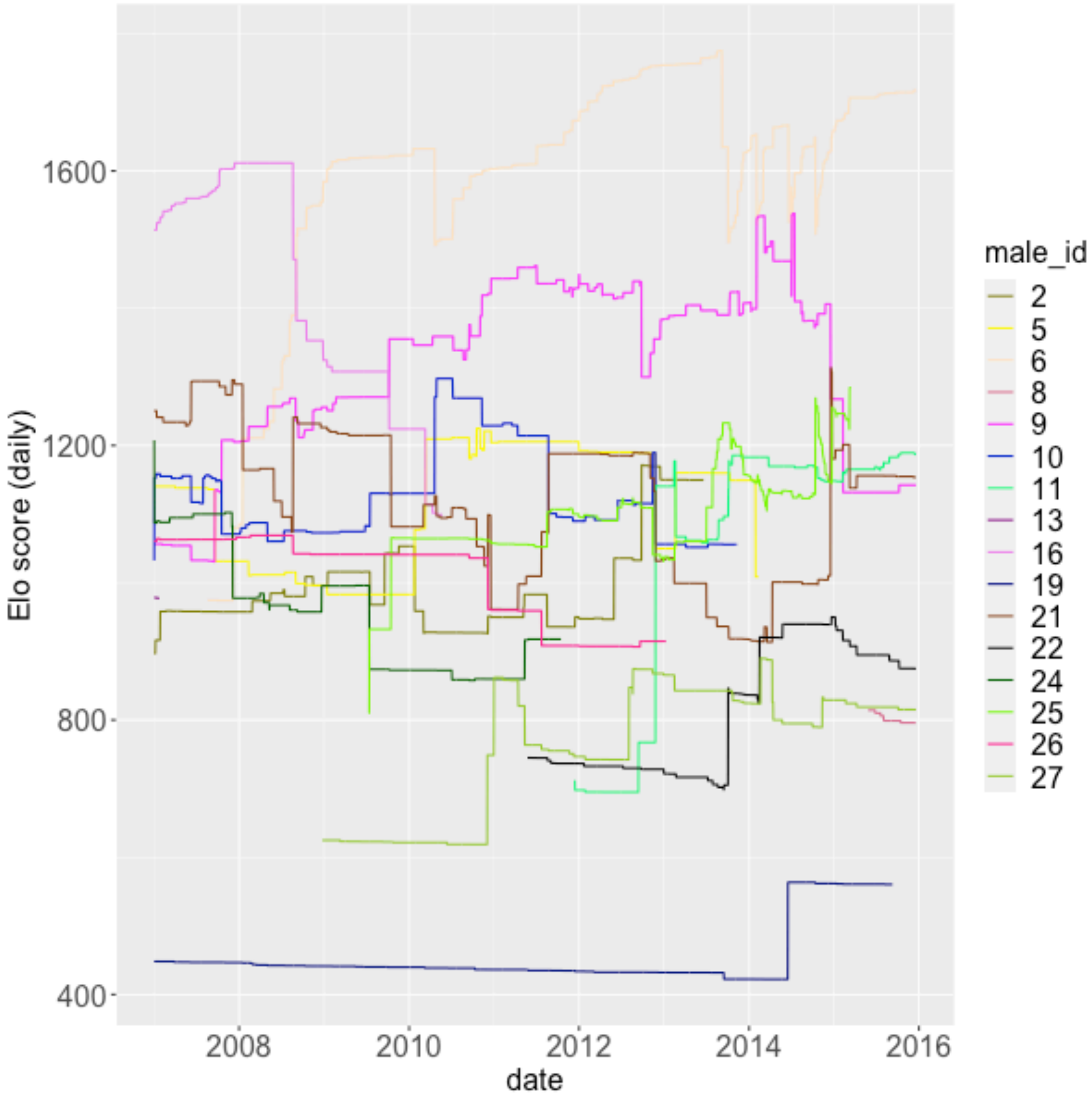


Figure S3.9

Male Elo scores (≥ 15 years old) from 2007-2015



APPENDIX C

SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Table S4.1

Parameter estimates and model diagnostics for all models

Note. Parameter estimates for all models, including posterior means and standard deviations. Also included are two model diagnostics: effective sample size (ESS) and the Gelman-Rubin convergence diagnostic (Rhat)

Model	Parameter	Mean	SD	ESS	Rhat
Outcome: Association Predictor: Association with Adult Males while Immature	α_z Intercept	-1.65	1.34	4070	1.00
	α_g Intercept	-2.99	0.23	2295	1.00
	β_z Rank	-0.81	0.49	4918	1.00
	β_g Rank	0.04	0.05	4133	1.00
	β_z Age	0.60	0.43	5426	1.00
	β_g Age	-0.08	0.05	5023	1.00
	β_z Maternal kinship	-0.76	1.82	7999	1.00
	β_g Maternal kinship	-0.13	0.42	2947	1.00
	β_z Rank difference	-0.25	0.56	4462	1.00
	β_g Rank difference	0.05	0.06	5172	1.00
	β_z Age difference	-3.11	1.07	3718	1.00
	β_g Age difference	-0.07	0.15	2454	1.00
	β_z Maternal kinship X age difference	-0.97	1.68	7257	1.00
	β_g Maternal kinship X age difference	0.10	0.24	3251	1.00
	β_z Maternal kinship X rank difference	0.20	1.83	10343	1.00
	β_g Maternal kinship X rank difference	-0.79	0.24	3884	1.00
	β_z Dyadic association index while immature	-1.14	0.76	4724	1.00
	β_g Dyadic association index while immature	0.09	0.06	3600	1.00
	β_z Joint days during target window	1.44	0.69	3907	1.00
	β_g Joint days during target window	-0.03	0.10	2485	1.00
Outcome: Grooming Predictor: Association with Adult Males while Immature	α_z Intercept	-1.88	0.97	1940	1.00
	α_g Intercept	-4.51	0.36	1591	1.00
	β_z Rank	-0.29	0.30	2378	1.00
	β_g Rank	0.06	0.09	2533	1.00
	β_z Age	-0.61	0.29	4232	1.00
	β_g Age	0.23	0.07	3540	1.00
	β_z Maternal kinship	-1.57	1.56	2936	1.00
	β_g Maternal kinship	-0.11	0.66	2234	1.00
	β_z Rank difference	0.12	0.36	2912	1.00

	β_g Rank difference	0.04	0.08	3986	1.00
	β_z Age difference	0.12	0.64	1921	1.00
	β_g Age difference	-0.17	0.24	1600	1.00
	β_z Maternal kinship X age difference	0.84	0.92	2982	1.00
	β_g Maternal kinship X age difference	-0.02	0.37	2386	1.00
	β_z Maternal kinship X rank difference	1.04	1.14	4467	1.00
	β_g Maternal kinship X rank difference	-0.61	0.30	3163	1.00
	β_z Dyadic association index while immature	-0.46	0.43	2890	1.00
	β_g Dyadic association index while immature	0.18	0.09	1768	1.00
	β_z Joint days during target window	0.48	0.49	2089	1.00
	β_g Joint days during target window	-0.21	0.16	1682	1.00
Outcome: Association Predictor: Association with Male Peers while Immature	α_z Intercept	-3.51	0.92	2343	1.00
	α_g Intercept	-3.00	0.24	1268	1.00
	β_z Rank	-0.04	0.26	2798	1.00
	β_g Rank	0.00	0.04	3941	1.00
	β_z Age	0.25	0.20	3859	1.00
	β_g Age	-0.05	0.03	2841	1.00
	β_z Rank difference	0.01	0.30	2653	1.00
	β_g Rank difference	0.05	0.06	2712	1.00
	β_z Age difference	-0.40	1.05	2156	1.00
	β_g Age difference	0.16	0.29	1289	1.00
	β_z Dyadic association index while immature	0.06	0.30	3364	1.00
	β_g Dyadic association index while immature	0.02	0.04	3896	1.00
	β_z Joint days during target window	-0.22	0.45	2355	1.00
	β_g Joint days during target window	0.04	0.10	1469	1.00
Outcome: Grooming Predictor: Association with Male Peers while Immature	α_z Intercept	-2.92	0.93	2375	1.00
	α_g Intercept	-4.69	0.42	1765	1.00
	β_z Rank	-0.70	0.24	2506	1.00
	β_g Rank	0.13	0.05	4138	1.00
	β_z Age	-0.03	0.25	2194	1.00
	β_g Age	0.03	0.05	2969	1.00
	β_z Rank difference	-0.10	0.26	3856	1.00
	β_g Rank difference	-0.10	0.06	3790	1.00
	β_z Age difference	-1.33	1.14	2220	1.00
	β_g Age difference	0.14	0.54	1741	1.00
	β_z Dyadic association index while immature	0.00	0.32	2075	1.00
	β_g Dyadic association index while immature	-0.02	0.07	2476	1.00
	β_z Joint days during target window	-0.52	0.46	2376	1.00
	β_g Joint days during target window	0.17	0.19	1889	1.00

APPENDIX D

APPROVAL OF CO-AUTHORS

Inclusion of the following co-authored manuscripts is approved by all collaborators:

CHAPTER 2: Ian C. Gilby

CHAPTER 3: Joseph T. Feldblum, Ian C. Gilby

CHAPTER 4: Carson M. Murray, Ian C. Gilby, Margaret A. Stanton

APPENDIX E

ETHICAL NOTE

Chimpanzees have been observed at Gombe National Park since 1960. This study followed U.S. and Tanzanian laws and was approved by the Tanzania Wildlife Research Institute, Tanzania National Parks, and the Tanzania Commission for Science and Technology. All animal protocols followed the guidelines for the treatment of animals recommended by the ASAB/ABS (2019).