The Development of Male Chimpanzee Reproductive Tactics

by

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Dedication

This dissertation is dedicated to Benny, a chimpanzee who somersaulted when he met steep hills.

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Abstract

Across the animal kingdom, males compete to mate with a limited number of reproductively available females. To ensure females mate with them, males often rely on their size and strength. They may fight their male rivals or use aggression to sexually coerce females. Both tactics are employed by adult male chimpanzees (*Pan troglodytes*). Yet, immature adolescent male chimpanzees, who cannot compete with adult males or intimidate females, nevertheless father offspring. In this dissertation, I investigate how they do so by testing the hypothesis that adolescent males form affiliative relationships with females. I proceed to determine whether males mate and reproduce with females with whom they form strong relationships. To obtain data to test these hypotheses, I studied 30 adolescent (9-15 y) and young adult males (16-20 y) in a community of 200 wild chimpanzees at Ngogo in Kibale National Park, Uganda, over 2 years. I documented their social interactions with other individuals, including their mothers and unrelated females. At the start of adolescence, males formed their strongest relationships with their mothers and received emotional and agonistic support from them. If their mothers died, males provided similar parental-like support to their own younger, orphaned siblings. Mothers and sons continued to affiliate as sons grew up, but by adulthood males formed their strongest affiliative bonds with individuals who were not their mothers. Some of these bonds were with unrelated females as well as with related and unrelated males. Males and females who formed strong bonds groomed often and equitably, reassured frequently, and kept track of each other during travel more often than other male-female pairs even when controlling for the time they spent together and the female's reproductive state. Despite the affiliative nature of these relationships, males also targeted their female partners for aggression. Affiliative and aggressive behavior displayed by males to females contributed to male mating success. The impact of aggression on mating success increased with male age and especially when they directed it toward females with whom they shared affiliative bonds. These results may help us to understand the evolution of social bonds between human females and males, which can involve affiliation, parenting by males, and sometimes coercive violence.

Chapter 1.

Introduction

This dissertation investigates the social development of adolescent and young adult male chimpanzees, who live on the outskirts of the male-bonded world that shapes chimpanzee society (e.g. Hayaki 1988; Kawanaka 1993; Mitani 2009; Nishida 2012; Watts 2018). I place special emphasis on social relationships between adolescent and young adult males and females. These females include mothers, who provide critical support to their sons as they gradually become independent over a prolonged period of development, and unrelated females with whom young males can mate and father offspring. How adolescent male chimpanzees reproduce poses a particularly interesting problem because they face stiff competition from adult males. To address these issues, I studied the behavior of 30 adolescent and young adult male chimpanzees at Ngogo in Kibale National Park, Uganda.

Background

Chimpanzees live in communities of 20 to 200 individuals, who fission and fuse to form temporary parties that vary in size and composition (Nishida 1968; Goodall 1986; Wood et al. 2017). While females typically emigrate at adolescence, males are philopatric and remain in their natal communities for life (Goodall 1986). Males are capable of reproducing during adolescence (between 8 - 15 y) when they display several changes in their behavior. Adolescent males start to move independently of their mothers and begin to follow adult males (Pusey 1983, 1990; Hayaki 1988). As they do so, they are especially submissive to adult males, who no longer show them the tolerance afforded to juveniles (Pusey 1990; Hayaki 1988). Adolescent males also begin to display aggression toward adult females, eventually out-ranking them by the time they become adults (Goodall 1986; Pusey 1990; Takahata 1990; Nishida 2011). After making the transition to young adulthood between 16 - 20 years old, males reach their full size. Yet they still remain on the outskirts of adult male social life and must work hard to integrate themselves into the male chimpanzee dominance hierarchy (Goodall 1986; Kawanaka 1993).

As adults, males strive for status to gain dominance over other males. A linear dominance hierarchy results (Bygott 1974; Goodall 1986; Muller 2002). Reproduction is influenced by male rank, with high-ranking males fathering more infants than low-ranking males (Constable et al. 2001; Boesch et al. 2006; Wroblewski et al. 2009;

Newton-Fisher et al. 2010; Langergraber et al. 2013). Adolescent males, however, manage to reproduce despite their low rank, fathering 5-12% of offspring in communities that have been studied over long periods (Constable et al. 2001; Boesch et al. 2006; Wroblewski et al. 2009; Newton-Fisher et al. 2010; Langergraber et al. 2012, 2013).

Because adolescent and young adult males cannot compete with adult males for mating opportunities, they are likely to employ alternative reproductive strategies that target females themselves. Such strategies have been well-documented in adult male chimpanzees who are aggressive to females and use force to coerce them to mate (Smuts & Smuts 1993; Muller et al. 2007, 2011; Feldblum et al. 2014; Kaburu et al. 2015; but see Stumpf & Boesch 2010). Aggression is nonrandom, with males behaving aggressively toward older, parous females who they prefer as mating partners (Muller et al. 2006, 2007). Targeted aggression toward these females may reflect long-term relationships between particular male-female pairs. Males direct heightened aggression to specific estrous females (Muller et al. 2011), and males who display frequent aggression to a cycling female outside of her maximally swollen period are likely to sire her offspring (Feldblum et al. 2014). Despite our extensive knowledge about adult male aggression toward females, scant information exists about the development of male sexual coercion.

Adult male chimpanzees use affiliative as well as aggressive tactics to mate with females. Males who associate often with females when they are not cycling mate with them (Matsumoto-Oda 2002). In addition, some male and female chimpanzees range over similar areas of the community territory and associate frequently (Langergraber et al. 2013). These associations are not as conspicuous as the strong social bonds formed between male chimpanzees (Gilby & Wrangham 2008; Mitani 2009; Machanda et al. 2013). Nevertheless, they appear to influence male reproduction as males and females who associate, produce offspring together (Langergraber et al. 2013). Currently available data provide few clues about how selective associations between adult males and females develop.

This study

The preceding discussion highlights two major gaps in our understanding of adolescent male chimpanzee behavior. First, when do males begin to use aggression to coerce females to mate with them? Second, do young male chimpanzees mate and reproduce by forming affiliative relationships with females? To investigate the social development of male chimpanzees and how affiliative and aggressive social interactions affect their ability to reproduce, I conducted a systematic study of adolescent and young adult males at Ngogo. The Ngogo chimpanzee community is the largest documented in the wild, and the chimpanzees there have been studied continuously by John Mitani and David Watts since 1995 (Wood et al. 2017). When I began my research in 2013, there was an exceptionally large cohort of adolescent males at Ngogo, providing an ideal opportunity to examine the tactics that they employ to obtain matings with females.

During my first visit to Ngogo in 2013, I witnessed an adolescent male attack an adult female seemingly without provocation. This incident sparked my interest in why he did so. During a subsequent 3-month field season in 2014, I learned to identify the Ngogo chimpanzees and to navigate their territory. I also started to collect pilot data for this study, focusing on adolescent (9-15 years) and young adult males (16-20 years) to answer questions about the development of male chimpanzee reproductive tactics. I excluded males over 20 years of age after conducting focal observations of six males between the ages of 21-23. In keeping with the results derived from prior studies (Goodall 1986; Kawanaka 1993; Watts 2018), I found that their behavior was conspicuously different from males just a few years younger. Male chimpanzees in their early twenties frequently engaged in direct contests with other adult males. In contrast, some males younger than 20 years old continued to remain on the outskirts of male chimpanzee competitive and social life (e.g. Hayaki 1988; Pusey 1990; Kawanaka 1993).

During my 2014 pilot season and in the spring of 2015, I refined the behavioral observation protocol employed in this study. Here I made a tradeoff between conducting relatively short focal observation sessions to maximize the number of males

I could sample with longer all-day follows during which I would be able to record the relaxed affiliative behaviors my male subjects would sometimes display with individual females. After piloting both approaches and noting that adolescent males often moved back-and-forth between large groups of adult males and mostly female parties containing their mothers, I determined that 3-hour following sessions permitted me to capture the range of social interactions engaged in by these males. This sampling regime also allowed me to collect sufficient data on my 30 male subjects across the 2-year study period. I initiated data collection for this study in the summer of 2015, returning for a continuous 15-month field season from June 2016 to August 2017.

During this research two major events impacted the lives of the Ngogo chimpanzees. One event was a community fission. The fission took place gradually over about 2.5 years starting in July 2015. The split was marked by members of one community killing a male from the other group in 2018, two months after the completion of this study. Throughout most of this study, male and female chimpanzees who now live in two different communities created by the fission affiliated and maintained social relationships. Thus, the community fission is not discussed at length in this dissertation.

The second event was a respiratory outbreak in January 2017 that resulted in the disappearance and presumed death of 25 chimpanzees, including the mothers of four of my male focal subjects, 3 who were adolescent and one who was a young adult

(Negrey et al. 2019). These deaths gave me an opportunity to investigate how sons altered their behavior after maternal loss. The lives of my young male subjects changed profoundly after their mothers died, as they started to take on parent-like roles for their younger siblings. The evolving relationships between these males and their siblings provided insight into how kinship influences the behavior of adolescent male chimpanzees and led me to examine the social relationships between adolescent and young adult males and their mothers and siblings. Findings derived from these studies provide the context to understand how adolescent male chimpanzees build relationships outside of their families, including with unrelated females.

The results of my research are presented in four chapters in this dissertation. Chapter 2 describes relationships between males and their mothers and how these change between them from the start of adolescence and start of prime adulthood. I investigate affiliative interactions between mothers and their sons, including grooming, the maintenance of spatial proximity, and traveling together as well as supportive behaviors such as reassurance and agonistic support during conflicts. Chapter 3 describes how the lives of four young males changed following the death of their mothers. I document changes in the social relationships between these males who were orphaned during the January 2017 respiratory outbreak and their younger siblings. When their mothers died, these adolescent and young adult male chimpanzees displayed heretofore undescribed caregiving behavior to their younger siblings. In Chapter 4. I demonstrate that adolescent and young adult males form affiliative relationships with unrelated females. These relationships increased in strength and number as males grew older. Although males and females in these strongly bonded pairs groomed frequently and relatively equitably, reassured often and kept track of one another during travel, males also targeted their female partners for aggression. In Chapter 5, I show the aggressive and affiliative aspects of these relationships affect male mating and reproduction. This chapter also reveals how male mating behavior and reproduction change with male age.

All research protocols reported here were granted exemption by the Institutional Animal Care and Use Committee at the University of Michigan. Work conducted in Uganda was approved by the Uganda National Council for Science and Technology (NS488), and the Uganda Wildlife Authority (EDO-35-01).

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Chapter 2

Social Relationships Between Chimpanzee Sons and Mothers Endure but Change During Adolescence and Adulthood

Note on Publication

Chapter 2 has been submitted for publication as a co-authored research article. My co-author is Dr. Aaron Sandel (A.S.), assistant professor of anthropology at the University of Texas at Austin. A.S. contributed to the development of the study, to behavioral data collection, and to the writing of the manuscript.

Abstract

Mothers provide indispensable care for infants in many mammalian species. In some long-lived species, the maternal - offspring bond persists after infancy with mothers continuing to provide resources and social support to their adult progeny. In male-philopatric chimpanzees, adult males form their strongest bonds with other males, and mothers are limited in their ability to help them. Few studies have examined social relationships between mothers and their adolescent and adult sons. To determine how maternal bonds with their sons change as males transition to adulthood, we investigated social interactions and relationships between 29 adolescent and young adult male chimpanzees (9-20 years) and their mothers at Ngogo in Kibale National Park, Uganda. All males under 12 years old had their mother as their top grooming and proximity partner, as did one third of the young adult males. As males grew older, the amount of time they associated with, maintained proximity to, groomed with, and kept track of their mothers while traveling decreased. When males were together in the same party as their mothers, however, young adult males interacted with their mothers as frequently as did adolescent males. In contrast to adult sons, adolescent sons cried when separated from mothers and relied on their mothers for agonistic support and reassurance after conflicts. These findings indicate that the chimpanzee maternal – offspring bond continues through adolescence and adulthood,

with mothers remaining occasional social companions for most sons and frequent companions for some.

Introduction

Mammalian mothers provide care that is critical to the survival of their offspring. Mammals are nursed by their mothers from birth, and once weaned, individuals in some species continue to rely on their mothers for food and social support (e.g. juvenile hyenas (*Crocuta crocuta*): Watts et al. 2009). If mothers die, weaned orphans experience lifelong problems, including decreased survival, reproduction, growth, health, dominance status, and emotional development compared to their peers (e.g. Asian elephants (*Elephas maximus*): Ladenphera et al. 2016; baboons (*Papio cynocephalus*): Tung et al. 2016; red deer (*Cervus elaphus*): Andres et al. 2013, humans (*Homo sapiens*): Cerel et al. 2006; bonobos (*Pan paniscus*): Clay and deWaal 2013; chimpanzees (*Pan troglodytes*): Nakamura 2014; Walker et al 2018; Samuni et al. 2020; Stanton et al. 2020). In some species, mothers retain bonds with their offspring and continue to contribute to their welfare in adulthood (e.g. baboons: Silk et al. 2006; bonobos: Surbeck et al. 2011; orca whales (*Orcinus orca*): Brent et al. 2015). For example, female baboons and elephants keep their mothers as strong social partners throughout life and raise more surviving offspring if they maintain bonds with their mothers (Silk et al. 2006, 2009; Ladenphera et al. 2016).

Because most mammals display female philopatry, mothers typically retain social bonds with their adult daughters and break them with their adult sons. Humans are a notable exception (Chapais 2008), as is one of our two closest living relatives, bonobos. Bonobo mothers remain their sons' closest companions throughout life and also promote their reproduction by supporting them to achieve high dominance rank and obtain mating opportunities with females. Bonobo mothers can serve as valuable allies for their adult sons in these ways because they can dominate males (Ihobe 1992; Furuichi 1997, 2011; Surbeck et al. 2011; Surbeck et al. 2019).

Mothers appear to have less to offer their adult sons in the male-dominated world of our other close relatives, chimpanzees. Adult male chimpanzees form their strongest social bonds with other adult males, who are their most effective allies (Goodall 1986; Langergraber et al. 2007; Gilby and Wrangham 2008; Mitani 2009; Machanda et al. 2013). Adult males help other males as they strive for status, and high-ranking males reproduce more than low-ranking individuals (Bygott 1974; Nishida 1983; Nishida and Hosaka 1996; Boesch et al. 2006; Wroblewksi et al. 2009; Newton-Fisher et al. 2010; Langergraber et al. 2013).

Although adult male chimpanzee reproductive success is not affected by maternal presence as it is in bonobos (Surbeck et al. 2019), chimpanzee mothers begin as the closest social partners of their sons when they are young. As infants, sons are carried and nursed by their mothers, and they travel in the same parties, or fluid subgroups, with them almost constantly during juvenility (van Lawick-Goodall 1968; Pusey 1983, Goodall 1986; Pusey 1990). During adolescence (8 – 15 years), male chimpanzees start to become independent of their mothers, traveling apart from them

(Pusey 1983; Goodall 1986; Hayaki 1988; Pusey 1990). Despite loosening ties with their mothers, adolescent males still appear to reap benefits from them, as maternal presence improves growth and survival of sons until the start of adulthood at around 16 years of age (Goodall 1986; Nakamura 2014; Samuni et al. 2020; Stanton et al. 2020).

Clarifying whether and how mothers continue to aid their adolescent sons is difficult because scant data exist regarding how chimpanzee mothers interact with their sons as they transition to adulthood. Pusey (1983), Nishida (1988), and Takahata (1990) each report observations of single mother-son pairs who groomed frequently and occasionally reassured each other after conflicts. In addition, adult sons are consistently described to interact differently with their mothers than with other female chimpanzees. Males rarely mate or show interest in mating with their mothers, and mothers are less fearful of their grown sons than they are of other males (Pusey 1983; Goodall 1986; Takahata 1990; Wroblewski et al. 2009; Walker et al. 2016). In addition, mothers only rarely give pant grunts, calls that indicate subordination, to their adult sons or receive aggression from them.

In the unusually large Ngogo chimpanzee community in Kibale National Park, Uganda, females live a long time (Wood et al. 2017), potentially due to an abundant food supply (Potts et al. 2020). Consequently, several mothers there reside together with their adult male sons. Abundant food also results in the Ngogo chimpanzees forming large, mixed-sex subgroups or parties containing both mothers and sons

(Langergraber et al. 2009, 2013; Wakefield 2013). Taken together, these factors create an ideal opportunity to investigate how chimpanzee mothers interact with their sons as they transition from adolescence to adulthood. In this paper, we describe social interactions and relationships between adolescent and young adult male chimpanzees and their mothers at Ngogo. We document how certain aspects of the maternal-infant bond endure while others change as chimpanzee sons mature and cross the threshold to adulthood.

Methods

Study Site and Subjects

Research took place at Ngogo in Kibale National Park, Uganda, a mid-altitude rainforest (Strushaker 1997). Members of the Ngogo chimpanzee community occupy a territory of approximately 35 square kilometers and have been followed continuously since 1995. During this study, the community size ranged between 180 - 219 individuals, including 29 adolescent (8-15 y) and young adult (16-20 y) males whose mothers were alive. Together we conducted 1,570 hours of focal observations (mean = 54 hours per male; SD = 21 hours) of adolescent (9-15 y) and young adult (16-20 y) males over three years. A.S. followed 13 males between August 2014 and August

2015, while R.R. followed 25 males between June 2015 to August 2015, and June 2016 to August 2017. Nine of these males were subjects of both A.S. and R.R (Table 1).

Table 1. Adolescent and adult male chimpanzee focal subjects and their mothers.

Male	Mother	Year of Birth	Observers
Hawkins	Anderson	1995	A.S.
Peterson	Aretha	1995	A.S.
Evans	Sills	1996	A.S.
Wayne	Kundry	1996	A.S.
Hicks	Harper	1997	A.S., R.R.
Haden	Lita	1999	A.S., R.R.
Abrams	Callas	1999	A.S., R.R.
Lovano	Fitzgerald	1999	A.S., R.R.
Wilson	Kidman	1999	A.S., R.R.
Buckner	Lucia	2000	A.S., R.R.
Benny	Cecilia	2000	A.S., R.R.
Chopin	Violetta	2001	R.R.
Barron	Sutherland	2001	A.S., R.R.
Booker	Sills	2002	A.S., R.R.

Bosko	Julianne	2003	R.R.
Murray	Senta	2004	R.R.
Jarman	Callas	2005	R.R.
Elton	Kidman	2005	R.R.
Billy Bragg	Rusalka	2005	R.R.
Orff	Sutherland	2005	R.R.
Yo Yo	Cecilia	2006	R.R.
Fleck	Sarah	2006	R.R.
Damien	Kanawa	2006	R.R.
Dylan	Fitzgerald	2006	R.R.
Nelson	Anderson	2007	R.R.
Gus	Sills	2007	R.R.
Cannonball	Sigourney	2007	R.R.
Williams	Bacall	2007	R.R.
Larson	Fleming	2007	R.R.

Behavioral Observations

It was not possible to record data blind because our study involved focal animals in the field. Focal observation sessions typically lasted 1 hour for A.S. and 3 hours for R.R. After these, we switched to new focal subjects. If no other focal subject was present, A.S. left to search for other chimpanzees, while R.R. remained with her current subject for up to 5 hours before leaving to search for a new one. In rare instances when there were no other focal subjects available, she followed her current focal individual for more than 5 hours. The different observation protocols reflected our distinct research projects. A.S. studied male-male relationships and stayed with large male parties, while R.R. studied male-female relationships and her longer sessions permitted her to follow the same young male as he moved in and out of parties that contained females (Langergraber et al. 2009; Wakefield 2013).

We recorded chimpanzees in association with focal subjects at one-hour intervals. Chimpanzees in view of each other were defined to be in association (i.e. in the same temporary subgroup, or "party"). Individuals within 5 meters proximity to focal subjects were recorded every 10 minutes, and the amount of time focal subjects gave and received grooming was noted to the nearest second. During focal follows, R.R. recorded other behaviors that occurred between her focal subjects and their mothers (n = 25), including vigilance during travel, whimpering or crying behavior when separated, reassurance, and agonistic support. Travel vigilance included behaviors that allowed mothers and sons to maintain association while traveling (Pusey 1983; Gruber & Zuberbuhler 2013; Reddy and Mitani 2019). They involved cases where a male followed, waited for, or looked back for his mother while traveling or she followed, waited for, or looked back at him. Reassurance behaviors consisted of gentle touches, mouthing, kissing, hand-holding, embracing, genital-rubbing, and mounting between pairs (van Lawick-Goodall 1968). We also recorded instances where focal chimpanzees supported or received support from their mothers when they were targets of aggression. Aggression involved displays, threats, chases, charges, and attacks involving contact aggression (van Lawick-Goodall 1968). Crying included instances like those described by Pusey (1983) and Hayaki (1988) where sons separated from their mothers or became separated from them, then suddenly began to whimper while searching, running back and forth, standing bipedally, sometimes erupting into screams until they found their mother or she returned to them. Play involved individuals gently mouthing each other, tugging on each other's hands and feet, wrestling, and chasing each other, often while laughing (van Lawick-Goodall 1968; Nishida 2012). We also recorded dominance and sexual behavior expected to occur frequently between male and unrelated female chimpanzees, but not between mothers and sons (e.g. Pusey 1983; Takahata 1990). These included the preceding aggressive behaviors, mating, and pant grunts, which are distinctive calls given by low-ranking individuals to higher-ranking individuals (Bygott 1974).

Data organization and analysis

Male age

In the following analyses, we consider male age as a continuous variable, calculating it as the midpoint of a male's age during the years he was followed during the 2014-2015 or 2015-2017 study period. Males followed in both periods were entered twice in the following analyses. One entry included his age and behavior with his mother during 2014-2015, while the other included his age and behavior with his mother during 2015-2017. In some of the following descriptions, we assigned each male to an age category based on the midpoint of his age across each study period. Following Goodall (1986), each male was designated as a young adolescent male (9-11 years old), a mid-to-late adolescent male (12-15 years old), or a young adult male (16-20 years). A male was assigned to these categories based on the midpoint of his age during the time period he was studied. Most males remained in the same age class from 2015-2017, making it appropriate to categorize them in this way for descriptive purposes (Table 1).

We used a model comparison approach to examine whether male age influenced maternal-son behavioral interactions. We compared models that included the following social outcome variables: 1) association, 2) proximity, 3) grooming, and 4) travel vigilance. For each of these outcome variables, we compared model(s) that included male age as a main predictor to a control model. The control models excluded male age and contained observation time as the main predictor as well as male and mother identity as random intercepts. All models assumed a negative binomial distribution, based on the distribution of our outcome variables, which were all counts. We used Akaike's information criterion, corrected for small sample size (AICc), to compare the efficacy of the models with male age as a predictor to the controls. We report coefficient estimates and standard errors for all models. We examined the effect of male age on each of the preceding social behaviors in additional analyses outlined below.

Association

We investigated how association patterns between mothers and sons changed with male age. We report the mean percentage of following episodes that focal males spent in association with their mothers. We then evaluated how a male's age influenced the amount of time he spent in association with his mother by conducting a generalized linear mixed model analysis (GLMM) that assumed a negative binomial distribution. In this analysis, the outcome variable was the number of times a male was observed in association with his mother and the main effect predictors were the male's age and observation time defined as number of focal following episodes of each male. We included observer and male identity as random intercepts in this model.

Proximity, Grooming, & Travel Vigilance

Next, we investigated the effect of male age on the amount of time males and their mothers spent in close proximity and groomed, as well as whether it influenced the degree to which males and their mothers kept track of each other while traveling by displaying vigilance. First, we determined where mothers “ranked” among all individuals with whom their sons engaged in the each of the three preceding behaviors. If a son maintained proximity to, groomed with, or engaged in travel vigilance with his mother more times than any other individual, she was considered his top partner for that behavior. Second, we evaluated how a son’s age influenced the frequency with which he and his mother behaved in the preceding ways. Here, we wanted to determine the overall frequency of interaction between mothers and sons as well as whether males increased their levels of proximity, grooming, and vigilance with their mothers during times when they were together. Thus, we calculated the rates of proximity (% of scans), grooming (min/hr), and travel vigilance (instances/hr) for mothers and sons across all of our focal observations and during times when they were together and associating with their mothers. We determined mean “total” and “when in association” rates of the preceding behaviors for young adolescent, mid-to-late adolescent, and young adult males. For proximity and grooming values, we combined our data as we did for association measures. For travel vigilance, we included only R.R.’s data (n = 25 males, age 9 – 20 y), as only she recorded this behavior.

Next, we evaluated how a male's age influenced affiliation with his mother by conducting three GLMM analyses where the outcome variable was the: 1) number of scans a male was observed in proximity to his mother, 2) the number of minutes a male groomed or received grooming from his mother, and 3) the number of times a male or his mother showed vigilance for the other during travel. We used male age as the main predictor in these three models. To compare how males affiliated with their mothers across all of our observations to how they did so when they were associating in the same subgroup together, we conducted two analyses using each of the three preceding outcome variables. One analysis included the time a mother and son spent in association as a fixed effect, and in the other, this variable was not considered. In both sets of analyses, we controlled for observation time by including it as fixed effect and for male and observer identity by adding these as random intercepts. All models assumed a negative binomial distribution.

Reassurance, Agonistic Support, & Other Behaviors

We provide descriptions of the frequencies of reassurance behavior and agonistic support between mothers and sons in different age categories. We also report the frequencies of pant grunts, aggression, and mating between mothers and sons recorded during focal observations of our male subjects.

We conducted all analyses in R using the packages lme4, and MuMIn (Barton 2009; Bates et al. 2015; R Core Team 2017). To account for the varying scales of predictor variables in our multivariate analyses, we centred and standardized all predictors by using their z-scores, subtracting each data point from the mean and dividing this value by 2 times the standard deviation (Gelman & Hill 2007).

Results

Age

Age played an important role in all social interactions between sons and their mothers. Control models had model weights that were considerably lower than those that contained age as a predictor of behavioral frequency (Table 2).

Table 2. **Age**. Results of model selection analyses where outcome variables were the number of following episodes that a particular mother-son pair spent in: a) association, b) the number of scans they spent in proximity, c) the number of minutes they spent grooming, and d) the number of times they engaged in travel vigilance. Models are ranked by their AICc values. All models assumed a negative binomial distribution and contained male and mother identity as random intercepts. In each

set of comparisons, “mod0” indicates the control model that did not include age as a predictor, while the model(s) labeled “mod1” include age as a predictor and the model(s) labeled “mod2” include age and the time a male and his mother spent in association

a) association

	intercept	obs time	age	AICc	delta	weight
mod1	2.91	0.45	-0.87	263.34	0.00	1.00
mod0	2.98	0.47	NA	286.91	23.57	0.00

b) proximity

	intercept	obs time	age	association	AICc	delta	weight
mod2	2.43	-0.22	-0.52	1.48	297.54	0.00	1.00
mod1	2.39	0.24	-1.49	NA	309.63	12.09	0.00
mod0	2.54	0.27	NA	NA	329.16	31.62	0.00

c) grooming

	intercept	obs time	age	association	AICc	delta	weight
mod1	3.47	0.53	-1.88	NA	337.10	0.00	0.63
mod2	3.43	0.05	-0.82	1.17	338.33	1.23	0.34
mod0	3.46	-0.04	NA	NA	343.00	5.90	0.03

d) travel

vigilance

	intercept	obs time	age	association	AICc	delta	weight
mod2	1.39	0.57	-0.10	1.27	150.15	0.00	0.62
mod1	1.38	1.05	-1.09	NA	151.49	1.33	0.32
mod0	1.39	0.81	NA	NA	155.01	4.86	0.06

Association

All 29 adolescent and young adult male chimpanzees associated with their mothers. Younger males did so more frequently than older males (Table 3). On average, young adolescent males (9 – 11 y) were together with their mothers 74% (SD=16%) of the time (n = 9 males, n = 439 following episodes), mid-to-late adolescent males (12 – 15y) 46% (SD=18%) of the time (n = 9 males, n = 616 following episodes), and young adult males 26% (SD=13%) of the time (n = 11 males, n = 825 following episodes). A GLMM analysis revealed that with each unit increase in male age, the number of times males associated with their mothers decreased by a factor of 0.41 (Table 3, Figure 1).

Table 3. **Association**. Results of a GLMM analysis where the outcome variable is the number of times a male was in association with his mother. Estimate sizes of main predictors and their standard errors are displayed. The model included male identity and observation period as random intercepts and assumed a negative binomial distribution (n = 29 males).

	Estimate	Std. Error
intercept	2.91	0.07

male age	-0.87	0.14
number of following episodes	0.45	0.12

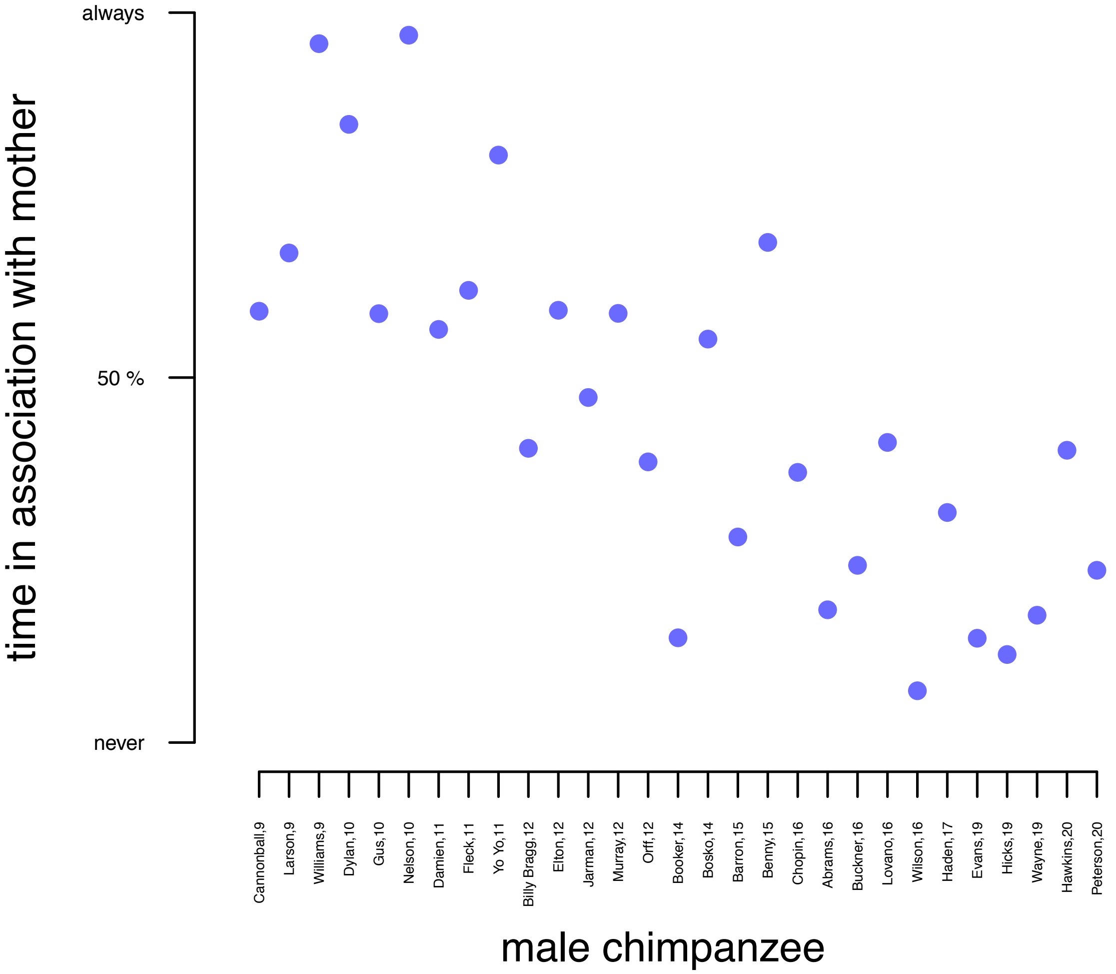


Figure 1. Time in association between adolescent and young adult males and their mothers (n = 29 males)

Proximity

The majority of adolescent and young adult males were observed in close spatial proximity to their mothers during focal observations (90% = 26/29 males). Young males maintained proximity to their mothers more often than did older males. All but one (89% = 8/9) young adolescent males had their mother as their first or second ranked proximity partner compared to 67% (6/9) of mid-to-late adolescent males and 18% (2/11) of young adult males. On average, young adolescent males were within 5 meters of their mothers in 24% (SD = 12%) of scans (range = 8 to 42%, n = 2,210 scans), mid-to-late adolescent males in 8% of scans (SD=5%, range = 2 to 17%, n = 3,334 scans), and young adult males in only 2% of scans (SD=2%, range = 0 to 7%, n = 4,867 scans). Only three males were never observed in proximity to their mothers during focal follows and all were young adults. A GLMM analysis indicated that the amount of time a male spent in close proximity to his mother decreased by a factor of 0.22 with each unit increase in male age (Table 4a, Figure 2a).

Although older males maintained spatial proximity to their mothers less often than younger males, this difference was less pronounced during times mothers and sons were together in the same party. On average, young adolescent males were in proximity during 23% (SD=12%) of scans made while males associated with their mothers. In contrast, mid-to-late adolescent males were in proximity to their mothers in

14% of scans (SD=5%), while young adult males were in proximity in 7% of scans (SD=7%). A GLMM analysis that controlled for association time showed that the number of scans males were in proximity to their mothers decreased by a factor 0.52 with each unit increase in male age (Table 4b, Figure 2b).

Table 4. **Proximity.** Results of GLMM analyses where the outcome variable is the number of times a male was in close spatial proximity to his mother during a) all focal observations and b) when in association with his mother. Estimates sizes of main predictors and their standard errors are displayed. The model included male identity and observation period as random intercepts and assumed a negative binomial distribution (n = 29 males).

a) All focal observations

	Estimate	Std. Error
intercept	2.39	0.41
male age	-1.49	0.26
number of proximity scans	0.24	0.22

b) when in association with mother

	Estimate	Std. Error

intercept	2.43	0.26
male age	-0.52	0.30
number of proximity scans	-0.22	0.21

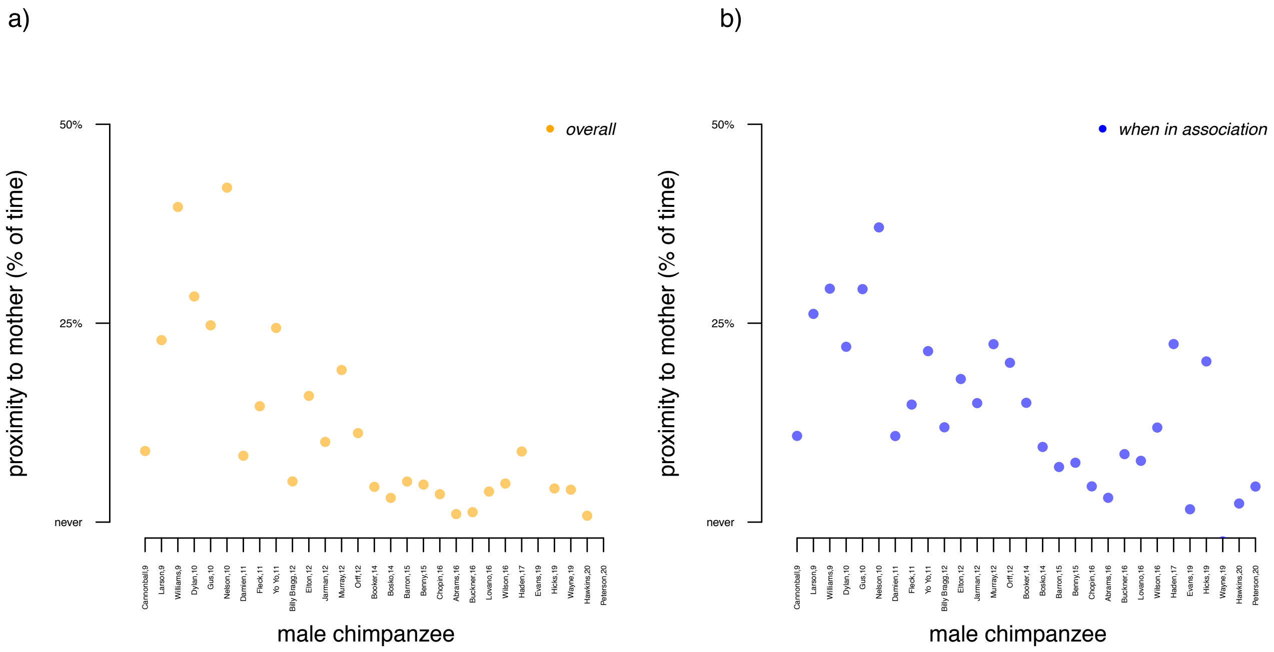


Figure 2. Time spent in proximity between adolescent and young adult males and their mothers during) all focal observations of male subjects and b) when male subjects and their mothers were in association

Grooming

The majority of adolescent and young adult males groomed with their mothers (93% = 27/29 males), and as with association and proximity, younger males groomed with their mothers more often than did older males. All young adolescent male subjects had their mother as their top grooming partner compared to 56% (5/9) of mid-to-late adolescent males, and 27% (3/11) of young adult males. On average, young adolescent males groomed with their mothers 2.7 minutes (SD=1.5) per hour of observation, mid-to-late adolescent males for 1.2 minutes per hour (SD=1.5), and young adult males for 0.3 minutes per hour (SD=0.5). The two males who were not observed to groom with their mothers during focal observations were young adults (Figure 2). A GLMM analysis indicated that for every unit increase in age, maternal - son grooming decreased by a factor of 0.15 (Table 5a, Figure 3a).

Although grooming with mothers decreased with male age, older males groomed with their mothers at frequencies similar to younger males when mothers and sons were together in the same party. For every hour they spent in association, young adolescent males groomed with their mothers for 2.8 (SD=1.5) minutes, mid-to-late adolescent males for 2.0 (SD=2.0) minutes, and young adult males for 1.1 (SD=1.45) minutes. Relative to how often males associated in the same party as their mother a male’s age did not influence how frequently he groomed with his mother (Table 5b, Figure 3b).

Table 5. **Grooming.** Results of GLMM analyses where the outcome variable is the number of minutes a male spent grooming with his mother during a) all focal observations b) when in association with his mother. Estimate sizes of main predictors and their standard errors are displayed. The model included male identity and observation period as random intercepts and assumed a negative binomial distribution (n = 29 males).

a) All focal observations

	Estimate	Std. Error
intercept	3.47	0.24
male age	-1.88	0.55
observation time	0.53	0.44

b) When in association with mother

	Estimate	Std. Error
intercept	3.43	0.23
male age	-0.82	0.94
association	1.17	0.85
observation time	0.05	0.56

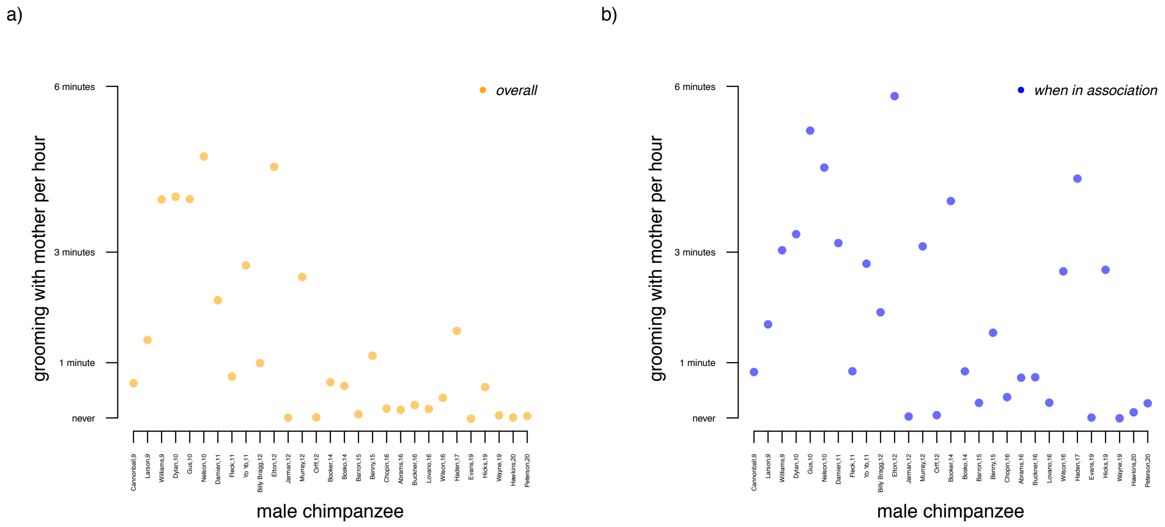


Figure 3. Time spent grooming between adolescent and young adult males and their mothers during) all focal observations of male subjects and b) when male subjects and their mothers were in association

Travel Vigilance & Crying

Males and their mothers kept track of each other while traveling by remaining vigilant. Travel vigilance occurred between 88% (22/25) of the adolescent and young adult males and their mothers. Younger males were vigilant slightly more often than were older males. Eight of nine (89%) young adolescent males had their mother as the individual they kept track most frequently while traveling, as did 88% (7/8) of mid-to-late adolescent males. Only 38% (3/8) of young adult males did so, however. On average, young adolescent males and their mothers displayed travel vigilance 0.26 times per hour (SD = 0.24), mid-to-late adolescent males and their mothers did so 0.09 times per hour (SD = 0.05), and young adult males and their mothers displayed travel vigilance 0.08 times per hour (SD = 0.09). For each unit increase in male age, the number of times males displayed travel vigilance with their mothers decreased by a factor of 0.33 (Table 6a, Figure 4).

While the attention sons paid to their mothers while traveling waned as males aged, this changed when they were together in the same party. On average, young adolescent males and their mothers displayed vigilance while traveling 0.25 (SD = 0.19) times for every hour they spent in association. Mid-to-late adolescent males did so 0.21 (SD = 0.18) times per hour in association, while young adult males displayed vigilance 0.23 (SD = 0.25) times per hour in association. A GLMM analysis that controlled for time spent in association showed that a son’s age did not influence how frequently he and his mother engaged in vigilance while traveling (Table 6b, Figure 4). When together, mothers and older sons kept track of one another at frequencies similar to mothers and younger sons. Furthermore, sons of all ages were especially keen of keeping track of their mothers in these pairs (21/22 = 95% of pairs). With one exception, males (21/22) followed or checked that their mothers were following them more often than did their mothers.

One third of the young adolescent males (33% = 3/9) and a quarter of the mid-to-late adolescent males (25% = 2/8) whimpered, cried, or screamed during focal observations when they became separated from their mothers. They did so 18 times. Young adult males never behaved in the same way.

Table 6. **Travel vigilance.** Results of a GLMM analysis where the outcome variable is the number of times a male showed vigilance to or received vigilance from his mother while traveling during a) all focal observations and b) when in association with his mother. Estimates of main predictors and their standard errors are displayed. The model included male identity and as a random intercepts and assumed a negative binomial distribution (n = 25 males).

a) All focal observations

	Estimate	Std. Error
intercept	1.38	0.21
male age	-1.09	0.41
observation time	1.05	0.45

b) When in association with mother

	Estimate	Std. Error

intercept	1.39	0.19
male age	-0.10	0.55
observation time	0.57	0.44
association	1.27	0.55

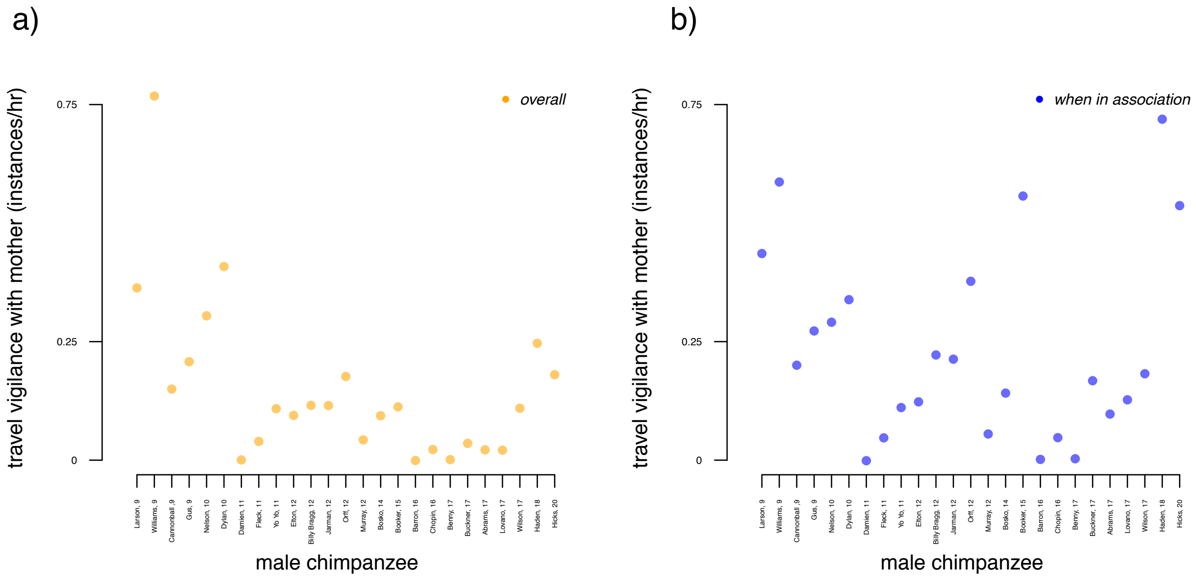


Figure 4. Instances per hour observed of travel vigilance between adolescent and young adult males and their mothers during) all focal observations of male subjects and b) when male subjects and their mothers were in association

Reassurance & Agonistic Support

Younger males displayed reassurance behavior with their mothers, but older males did so rarely. Virtually all of the young adolescent males (89% = 8/9) reassured with their mothers. They did so 10 times. In contrast, 38% (3/8) of the mid-to-late adolescent males displayed reassurance with their mothers doing so four times. A single young adult male (13% = 1/8) received reassurance from his mother once (Figure 5).

Most mothers provided agonistic support to their adolescent sons, but only a few mothers supported their older sons. About two thirds (67% = 6/9) of the young adolescent males received support from their mothers a total of 14 times. In contrast, 30% (3/9) of mid-to-late adolescent males received support from mothers a total of 5 times. Only one of the young adult males (13% = 1/8) was helped by his mother just once. Mothers defended their sons against aggression from adolescent and adult females as well as adult males. Twice mothers caused adult males to run away while defending their adolescent sons. Two times mothers and sons formed coalitions against a male who was directing aggression to both of them. In all 18 other cases a mother came to the aid of her son rather than vice versa (Figure 5).

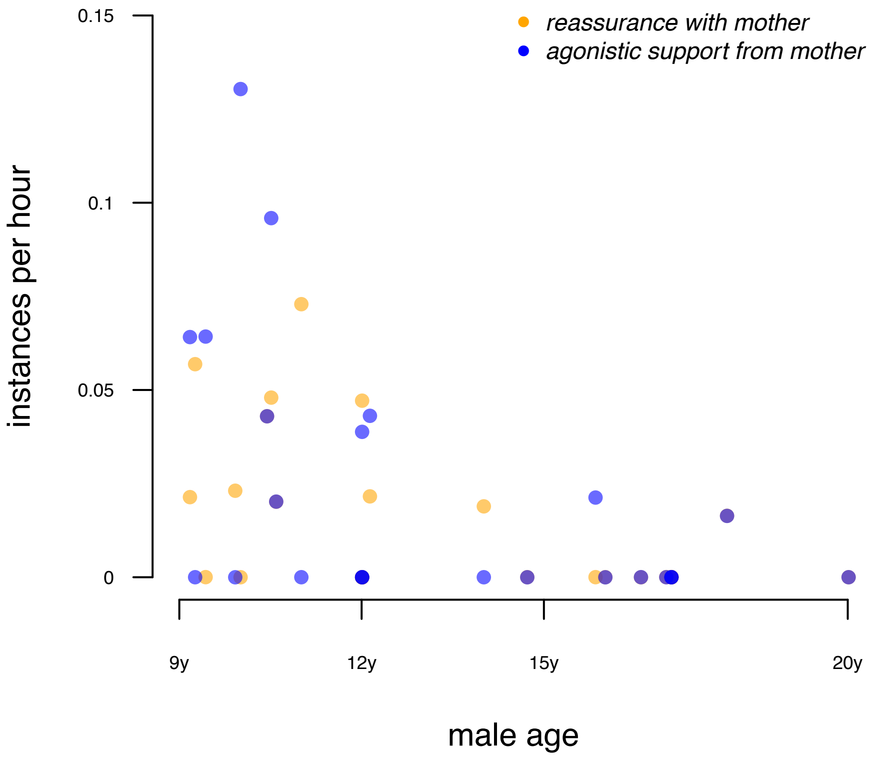


Figure 5. Instances per hour observed of a) reassurance and b) agonistic support between adolescent and young adult male subjects and their mothers by male age.

Additional affiliative and supportive behavior

Food-sharing occurred between two young adolescent males and their mothers and two mid-to-late adolescent males and their mothers a total of 25 times. Mothers and their adolescent and adult sons played rarely, with this taking place just 5 times between 3 young adolescent males and their mothers.

Dominance, aggression, and mating

No aggression, pant grunts, or mating occurred between mothers and their sons. Two young adolescent males interfered in their mothers' matings. One of these males, Cannonball, 9, did so 7 times, while Damien, 10, did so once.

Discussion

In the decade spanning the time male chimpanzees begin adolescence to the time they become prime adults (from 9 to 20 years old), the nature of the relationships with their mothers changes. Time spent associating, maintaining proximity to, grooming with, and keeping track of their mothers during travel decreases as males age, but even young adults continued to behave in these ways with their mothers at least occasionally. As in other chimpanzee communities, all males in this study who were younger than 12 years old had their mother as their "top" social partner, defined as the individual with whom they most frequently maintained proximity, groomed, and kept track of during travel (Pusey 1983, Pusey 1990). However, one-third of young adult males also had their mother as their top partner in all of these behaviors. In addition, when young adult males were together with their mothers in the same party, the frequency of grooming and travel vigilance increased to a point where they were comparable to frequencies displayed by adolescent males (Figures 3-4).

Although sons continued to affiliate with their mothers as they entered adulthood, their relationships differed from those between mothers and their adolescent sons. Like adolescent males, young adult males made efforts to associate with their mothers (Figure 6), but unlike young and mid-adolescent males, adult sons did not whimper or cry when separated from their mothers. The whimpering behavior that adolescents showed, also described by Pusey (1983) and Hayaki (1988), reflects both the psychological and emotional challenges male chimpanzees face as their lives change during adolescence. The fact that males "grow out" of this behavior may indicate how, as males approach and enter adulthood, the bonds they form outside of their maternal families increase in strength, number, and security (Pusey 1990; Goodall 1986; Hayaki 1988; Nishida 2011; Sandel et al. 2020; Reddy and Mitani 2020). Chimpanzees may also become more comfortable spending time alone in later adolescence and early adulthood, in contrast to juveniles and young adolescents, who, even if temporarily separated from their mothers, typically travel with other chimpanzees (Pusey 1990; Nakamura and Hitonaru 2019).

Figure 6. "Travel Vigilance." Abrams, 17, waits and looks back for his mother, Callas. Callas had recently returned from a sexual consortship that lasted 3 months

In addition to growing more comfortable while away from their mothers, male chimpanzees no longer rely on them as alliance partners as they approach adulthood. Adult males rarely received agonistic support or formed coalitions with their mothers or sought and received reassurance from them after a conflict. In contrast, the majority of adolescent males engaged in these behaviors. This shift reflects the male-dominated, male-bonded nature of chimpanzee society and the reproductive tactics employed by male chimpanzees (Mitani et al. 2000; Langergraber et al. 2007; Gilby and Wrangahm 2008; Mitani 2009; Machanda et al. 2013). Male chimpanzees achieve high status that confers reproductive benefits by forming short-term coalitions and long-term alliances with other males (Nishida, 1983; Nishida and Hosaka 1996). Their mothers cannot help them in this way, and males seek male partners instead. Notably, chimpanzees shift at this point in development from bonobos, where mothers and sons form strong affiliative bonds and alliances that provide reproductive opportunities for adult sons (Ihobe 1992; Surbeck et al. 2011, 2019).

Although chimpanzee mothers do not seem to affect the reproduction of their adult sons, they may do so while they are adolescents (Surbeck et al. 2019). Maternal status predicts the outcomes of conflicts between immature chimpanzees (Markham et al. 2015), and during adolescence, when males cannot compete in the male dominance hierarchy, they gain mating opportunities by forming affiliative relationships with females (Reddy and Mitani 2020). It is possible that mothers help their sons form bonds with other females and compete with other adolescent males for mating opportunities. Some evidence suggests mothers provide such benefits in male-philopatric, relatively egalitarian muriquis (*Brachyteles arachnoides*), where males do not always maintain strong bonds with their mothers as adults. Males who do so, however, are more successful reproductively than males who fail to retain maternal bonds (Strier et al. 2011). Investigating the role chimpanzee mothers play in influencing the mating and reproductive success of their adolescent sons will require additional long-term research.

Adolescent and adult sons may also provide fitness benefits to their mothers. Because old females are unable to retain bonds with their daughters, who have dispersed to other communities, adult sons remain as potentially important social partners. Their company may promote maternal health and longevity in ways similar to those documented in other species (e.g. Silk et al 2003). In addition, sons may help their maternal siblings survive, as chimpanzee mothers appear to seek the company of their adult sons when they have young infants vulnerable to within-group infanticide (Wellens 2017). Finally, the maintenance of bonds between chimpanzee mothers and their adult sons could facilitate the latter adopting their younger siblings, which increases their chances of survival, in the event that mothers die (Hobaiter et al. 2014; Reddy and Mitani 2019).

Unique ecological, social, and demographic factors may have led to the findings reported in this paper. For example, plentiful food at Ngogo may lead to increased female gregariousness and longevity (Langergraber et al. 2009; Wakefield 2013, Wood et al. 2017; Potts et al. 2020) and permit male chimpanzees at Ngogo to associate with their mothers as adults more frequently than adult males in other chimpanzee communities. The especially strong bonds we document here between adult males and their mothers, however, are consistent with anecdotal reports of close mother-adult son bonds in other groups (Pusey 1983; Nishida 1988; Takahata 1990). As in previous studies, there is considerable inter-individual variation in male chimpanzee behavior, and the full range of this variation is likely to be revealed in the especially large Ngogo community. For instance, males varied in how frequently they groomed with their mothers even though all males younger than 12 had their mothers as their top grooming partners. Determining the degree to which the results reported here reflect the behavior of chimpanzees in general or the unusual ecological, social, and demographic situation at Ngogo will require systematic studies across sites.

Results of this study inform our understanding of the nature of parent-offspring bonds in long-lived philopatric animals. The bond between chimpanzee males and their mothers last into adulthood, but diverge from the maternal – offspring bond in other long-lived, social species where such ties are among the strongest formed by adults (e.g. baboons: Silk et al. 2006; bonobos: Furuichi et al. 2011; elephants: Ladenphera et al. 2016). Chimpanzee mothers are only occasional affiliative companions for most of their adult sons, and the top social partners for just a few. Most chimpanzee adult males grow up to form their closest bonds with other adult males who, in contrast to many species who engage in cooperative behavior, are not necessarily close genetic kin (e.g. Langergraber et al. 2007; Mitani 2009; Sandel et al. 2020). Yet, during adolescence, while male chimpanzees grow independent from their mothers and strengthen their bonds with others, mothers provide important emotional and agonistic support that may contribute to health, growth, and survival (Nakamura et al. 2014; Samuni et al. 2020; Stanton et al. 2020) How mothers contribute to the development of their sons' relationships and reproduction during adolescence remains an important topic for future research.

Appendix: ***Ad libitum*** observations of rare behaviors between mothers and their adolescent and adult sons.

Agonistic support between mothers and adult sons

We once witnessed two adult sons come to the aid of their mother. An adult female, Aretha, was in the process of killing an adult female red colobus monkey by smacking it onto the ground repeatedly. As Aretha did this, adult male Garrison charged her. She screamed while holding the monkey and chased Garrison. Aretha's adult sons, Carter, 24, and Peterson, 19, then charged in and chased Garrison away. This resulted in Carter and Aretha both holding large portions of the monkey, which all family members shared.

Dominance, Aggression, and Mating Behavior between Mothers and Sons

We recorded one case of pant-grunting, 3 cases of aggression, one case of mating, and one attempted mating between mothers and sons.

We saw one mother, Garbo, pant grunt to her 21-year-old son, Hutcherson, in the following situation. Hutcherson, who during the preceding weeks had appeared to be challenging his older brother Richmond for the alpha position in the dominance hierarchy, made a non-directed display, running in a circle near Richmond, adult male Brownface, and Garbo. In response, Richmond climbed into a short tree several feet above the ground as did another adult male, Brownface. Meanwhile, Garbo screamed, pant grunted, and ran around on the ground. Hutcherson, piloerect, continued his charge for several more seconds, but then stopped. As he calmed down and no longer piloerect, he walked to his mother, who was sitting on the ground. He sat behind her and placed his hand on her shoulder. He rested it there for a moment then brought it down to meet his other hand in the middle of her back and started to groom her. At this time Richmond also came down from the tree. Throughout the three years of this study, Garbo and Hutcherson affiliated frequently, and this was the only time Garbo was seen to pant grunt to him. It was also the only time Richmond climbed in a tree to avoid Hutcherson charging.

We recorded aggression between two mother-adolescent son pairs and two mother-young adult son pairs *ad libitum*. Aggression between mothers and adolescent sons involved "tantrum-like" behavior on the part of the son (cf. Nishida 1990). In this case, adult female Callas hit her young adolescent son, Jarman, two times. This occurred once when Jarman was 9 years old, and he whimpered, screamed, and begged for a *Treculia africana* fruit on which Callas fed for a long time. Callas hit Jarman two years later when he behaved in a similar way as she fed on a *Neoboutonia macrocalyx* root. Jarman, already whimpering, screamed louder both times Callas hit him. Nine-year-old Dylan screamed while beating his mother, Fitzgerald, with both hands in the same way infants will scream and hit their mothers while being weaned (van Lawick-Goodall 1968, Nishida 1990). Dylan, however, had been weaned many years before. We did not see what (if anything) prompted Dylan's behavior, and Fitzgerald did not respond.

Aggression between mothers and adult sons occurred three times All three involved unusual incidents. In 2017, during a hostile encounter between chimpanzees in the Ngogo community's western neighborhood and the central-eastern neighborhood, western adult female Garbo ran directly toward her 45-year-old son, Monk, who has been a long-term occupant of the other neighborhood. She did so with her arms outstretched as chimpanzees sometimes do before embracing during reunions (cf. van-Lawick Goodall 1968). Monk jumped onto his mother's back and kicked her repeatedly while she screamed loudly. During a second encounter several weeks later, we saw Garbo lead a charge of Western males and females that resulted in several adult chimpanzees piling on top of Monk. Neither Garbo nor Monk had conspicuous physical injuries following these attacks.

A third case of aggression between a mother and her adult son occurred during an attempted mating. In 2015, 20-year-old Hawkins whimpered and stood with an erection behind his mother, Anderson, while she was in estrus. Anderson sat down and Hawkins continued to whimper and make begging gestures toward her. Anderson began to scream loudly and another adult male, Cash, arrived. This resulted in Hawkins moving away. Later that day, Hawkins charged Anderson. She screamed and chased Hawkins a long distance. He continued to run away even after Anderson stopped her chase.

One other time we witnessed sexual behavior between a male and his mother. Twenty-four year old adult male Carter approached and mated with his mother, Aretha. Aretha showed no distress or aggression toward Carter as he copulated with her.

Maternal involvement in boundary patrols

We also observed mothers to participate in territorial boundary patrols and engage their sons in an unusual way once. In this instance, Cecilia pushed her 10-year old son, Yo Yo, forward when he stopped and rested during a patrol while other chimpanzees continued to travel ahead. While Yo Yo lay on his stomach on the ground, Cecilia approached him from behind, put both hands under his rump, lifted it slightly, and pushed him forward. She did this twice, then Yo Yo stood and continued walking forward while she followed.

Chapter 3.

Social Relationships and Caregiving Behavior between Recently Orphaned Chimpanzee Siblings

Note on Publication

Chapter 3 is published in the journal *Primates* as a research article, co-authored by my dissertation chair, Dr. John Mitani (Reddy & Mitani 2019).

Abstract

When their mothers die, chimpanzees often adopt younger vulnerable siblings who survive with their care. This phenomenon has been widely reported, but few studies provide details regarding how sibling relationships change immediately following the deaths of their mothers. A disease outbreak that killed several females at Ngogo in Kibale National Park, Uganda, furnished an opportunity to document how maternal death influenced the social relationships of siblings. We describe social interactions between four adolescent and young adult males and their younger immature maternal siblings nine months before and eight months after their mothers died. We also show how the behavior of individuals in the four recently orphaned sibling pairs contrasts to the behavior displayed by chimpanzees in 30 sibling pairs whose mothers were alive. Following the death of their mothers, siblings increased the amount of time they associated, maintained spatial proximity, groomed, reassured, and consoled each other. During travel, younger orphans followed their older siblings, who frequently looked back and waited for them. Both siblings showed distress when separated, and older siblings demonstrated heightened vigilance in dangerous situations. Chimpanzees who were recently orphaned interacted in the preceding ways considerably more than did siblings whose mothers were alive. These findings suggest that siblings provide each other support after maternal loss. Further research is needed to determine whether this support buffers grief and trauma in the immediate aftermath

of maternal loss and whether sibling support decreases the probability that orphans will suffer long-term consequences of losing a mother if they survive

Introduction

In several species, individuals gain fitness benefits by developing social bonds with conspecifics (Silk et al. 2003, 2009, 2010; Cameron et al. 2009; Schulke et al. 2010). During youth, most mammals form strong and dependent relationships with their mothers. Mothers nurse their offspring during infancy and may continue to furnish support, protection, and comfort for many years after weaning them. Consequently, young mammals who lose their mothers often die. Orphans may survive, however, if they find another individual who provides care similar to a mother's. Maternal-like caregiving or "adoption" of such vulnerable orphans has been documented in the wild in many mammals (red squirrels: Gorrell et al. 2010; African wild dogs: McNutt 1996; bottlenose dolphins: Howells et al. 2009; elephants: Goldenberg & Wittemyer 2017; elephant seals: Riedman & LeBeouf 1982; savanna baboons: DeVore 1963; Altmann 1980; Hamilton 1982; hamadryas baboons: Kumer 1968; chimpanzees: Goodall 1968, 1983; Boesch et al. 2010; Hobaiter et al. 2014; bonobos: Surbeck et al. 2018; mantled howler monkeys: Clarke & Glander 1981; red howler monkeys: Agoramoorthy & Rudran 1992; Struhsaker 2008; ringtailed-lemurs: Gould 2000; black and white colobus monkeys: Dunham & Opere 2016; black-fronted titi monkeys: Casar & Young 2008). Caregiving by adopters includes nursing and food-provisioning, carrying, active vigilance during group travel, defense, grooming, and comforting behavior. Although individuals of different age and sex classes adopt orphans, older maternal siblings, if present, do so most often (e.g. African elephants: Goldenberg & Wittemyer 2017; baboons: Altmann 1980; Hamilton et al. 1982; Engh, et al. 2009; chimpanzees: Boesch et al. 2010; Hobaiter et al. 2014; red howler monkeys: Struhsaker 2008; ring-tailed lemurs: Gould 2000). This is unsurprising functionally and behaviorally. By helping their kin, older siblings can improve their inclusive fitness (Hamilton 1964), and in species where offspring maintain social relationships with their mothers after weaning, maternal siblings often share strong social bonds (reviewed in: Kapsalis 2004). Although sibling bonds are already strong, older sisters or brothers who adopt their younger siblings may take on a new parent-like role in the relationship, even if they are still immature (e.g. African elephants: Goldenberg & Wittemyer 2017; baboons: Altmann 1980; Hamilton 1982; Engh, et al. 2009; chimpanzees: Hobaiter et al. 2014). As they do so, their pre-existing relationships may intensify and change.

Young chimpanzees who lose their mothers are extremely vulnerable. They navigate a constantly changing social environment and require considerable amounts of care during long periods of dependency (Goodall 1986; Pusey 1983). Chimpanzees are born into social groups of 20 to 200 individuals, but the first bonds they form are with their mothers and maternal siblings (Goodall 1968; Pusey 1983; Goodall 1986). From birth, chimpanzees are carried, nursed, groomed, and gently touched and comforted by their mothers (Goodall 1968). They receive similar affection from their siblings, who are typically at least five years older (Pusey 1983). Mothers stop carrying and nursing their offspring when they are around five years old, but for several years thereafter they maintain close spatial proximity and groom with them. Mothers also defend their offspring against aggression and wait for them during group travel. Although chimpanzees constantly fission and fuse to form temporary parties that vary in size and composition (Nishida 1968), young chimpanzees travel almost constantly with their mothers and her other immature offspring (<12y) until mid-adolescence (Goodall 1968, 1986; Pusey 1983, 1990; Hayaki 1988). During late adolescence (~13y), female chimpanzees disperse to a new community, while males remain in their natal community for life, retaining relationships with their mothers but primarily traveling with other adult males, including their older maternal brothers (Goodall 1986; Hayaki 1988; Pusey 1990). As adults, maternal brothers often maintain strong, long-lasting relationships and cooperate in several different contexts (Langergraber et al. 2007; Mitani 2009).

When chimpanzee mothers die, immature orphans are often adopted by a maternal sibling if they have one (Goodall 1983; Boesch et al. 2010; Hobaiter et al. 2014). The care provided by siblings usually ensures that orphans survive, as long as they are at least 4.5 years old (Hobaiter et al. 2014). Several studies have documented adoption in chimpanzees and noted the remarkable care provided by both maternal relatives and non-relatives. This includes carrying, defense, food sharing, and even nursing (Goodall 1983; Boesch et al. 2010; Hobaiter et al. 2014). These reports, however, provide few detailed observations of how maternal siblings who adopt younger sisters or brothers behaved immediately before and after the deaths of their mothers.

A disease outbreak at Ngogo in Kibale National Park, Uganda (Negrey et al. 2019) furnished an opportunity to investigate the social behavior of orphaned siblings in the aftermath of maternal death. Specifically, we recorded how adolescent (9y - 15y) and adult (>15y) siblings, who already shared bonds with their younger, immature (<12y) siblings (Pusey 1983; Goodall 1986), transitioned to caregiver roles after their mothers died. To further contextualize this transition, we compare the behavior of orphans to the behavior of other siblings whose mothers were alive. We pay special attention to social interactions that may place emotional and cognitive demands on siblings who were caregivers and include several narrative anecdotes to illustrate these and how sibling relationships were influenced by maternal death.

Methods

Study Site & Subjects

Research took place at Ngogo in Kibale National Park, Uganda, a mid-altitude rainforest (Strushaker 1997). Members of the Ngogo chimpanzee community occupy a territory of approximately 35 square kilometers and have been followed continuously since 1995. The ages of most sub-adults and young adults in the community are known within one month to one year, while the ages of older individuals are estimated based on their genetic relationships to other individuals, physical appearance, and behavior (Wood et al. 2017). R.R. conducted behavioral observations over 20 months from June – August 2014, June - August 2015, and June 2016 to August 2017, with focal observations of adolescent (9 - 15y) and young adult (16 - 20y) males initiated in 2015.

During this study, the Ngogo chimpanzee community size ranged between 181 - 219 individuals, fluctuating due to immigrations, emigrations, births, and deaths. Twenty-five chimpanzee deaths occurred during a respiratory outbreak that began at the end of December 2016 and lasted through the start of February 2017 (Negrey et al. 2019). During the epidemic, 13 individuals (age 6 – 31yrs) lost their mothers. Nine of the 13 orphans were under the age of 12, and all but one had at least one surviving maternal sibling.

We studied the behavior of 20 adolescent and 10 young adult male chimpanzees who were part of a study on social development by R.R., and observed for at least 25 hours (mean ± SD = 47.8 ± 6.9 hours per focal subject). Of these 30 males, 24 had 1 or 2 maternal siblings present in the community who were immature and between 4 and 16 years younger than themselves. These younger immature siblings ranged from birth to 10 years old and included 27 individuals, seven of whom were the younger sibling of two focal males. Focal males and their younger, immature maternal siblings formed 34 unique pairs. Four of these pairs were orphaned during the outbreak and serve as case studies in this paper: Nelson (10 y old) and his sister, Amina (6 y old); Damien (11 y old) and his sister, Etta James (6 y old); Yo Yo (11 y old) and his sister Joya (6 y old); and Buckner (17 y old) and his brother Holland (7 y old). We observed these orphaned pairs 9 months prior to and 8 months following their mothers' deaths. The remaining 30 pairs had mothers who were alive throughout the study or for their entire lives. In one case, a focal male, Benny, disappeared and presumably died during the epidemic with his mother. Seven males had infant siblings who were born or died during the study (Table 7). All other sibling pairs were observed during the entire study.

In addition to focal observations, we report *ad libitum* observations of recent orphans who were focal subjects as well as observations of three additional sibling pairs following the deaths of their mothers: Rosa (11 y old) and her brother, Rich Bergl (4.5 y old), orphaned in 2015; Wayne (21 y old) and his brother, Bach (8 y old) orphaned in January 2017 during the epidemic; Rollins, (31 y old) and his sister, Etta James (6 y old) whose brother Damien (11 y old) was R.R.'s focal subject and was also orphaned during the epidemic. In a supplement, we describe the behavior and social relationships of recent orphans who lacked maternal sibling support.

Table 7. Focal chimpanzee subjects and their immature maternal siblings. All subjects are adolescent and young adult male chimpanzees studied between June 2015 and August 2017. Age values indicate ages in January 2017 rounded to the nearest year.

focal subject	age	mother	younger maternal siblings
Male orphans			
Nelson	10	Anderson (d. 2017)	Amina, (f, b. 2010)
Damien	11	Kanawa (d. 2017)	Etta James (f, b. 2011)
YoYo	11	Cecilia (d. 2017)	Joya, (f, b. 2011
Buckner	17	Lucia (d. 2017)	Holland (m, b. 2010) infant (b. 2015, d. 2017)
Males with living mothers			
Cannonball	9	Sigourney	Fricka (f, b. 2011)
Larson	9	Fleming	DiDonato (f, b. 2012) Whitman (m, b. 2016)
Williams	9	Bacall	Elvira (f, b. 2012) Caceres (f, b. 2016)
Gus	10	Sills	Denis (m, b. 2015)
Dylan	10	Fitzgerald	Pilar (f, b. 2013, d. 2017)
Fleck	11	Sarah	Salonen (m, b. 2012)
Billy Bragg	12	Rusalka	Flanagan (m, b. 2011)
Elton	12	Kidman	Cedar (m, b. 2013)
Jarman	12	Callas	Toshi (m, b.2011) infant (f, b. 2016, d. 2017)
Murray	12	Senta	Struhsaker (m, b. 2011) Junot (m. b. 2016)
Orff	12	Sutherland	Naidu (f, b. 2011)
Bosko	14	Julianne	Josipa (f, b. 2010) infant (m, b. 2015, d. 2016)

Booker	15	Sills	Gus (m, b. 2007) Denis (m, b. 2015)
Barron	16	Sutherland	Naidu (f, b. 2011)
Chopin	16	Violetta	Bobi Wine (m, b. 2010)
Abrams	17	Callas	Toshi (m, b.2011) infant (f, b. 2016, d. 2017)
Benny	17	Cecilia	Yo Yo, (m. b. 2006) Joya (f, b. 2011)
Lovano	17	Fitzgerald	Dylan (m, b. 2006) Pilar (f, b. 2013, d. 2017)
Wilson	17	Kidman	Cedar (m, b. 2013)
Haden	18	Lita	Muhammad Ali (m, b. 2015)

Behavioral Observations

R.R. recorded behavioral observations of chimpanzee maternal siblings during focal following episodes of adolescent and young adult males. Observation sessions typically lasted 3 hours. After following one focal chimpanzee for 3 hours, R.R. switched to a new subject. If no other focal chimpanzee was present, she remained with her current subject for 5 hours before leaving to search for a new one. In rare instances where no additional focal individual was available and there were no signs of other chimpanzees, males were followed for more than 5 hours.

R.R. recorded chimpanzees in association with her focal subjects every hour. Individuals within visual range of each other were defined to be in association. Chimpanzees in close spatial proximity to focal subjects, i.e. 5 meters, were noted every 10 minutes. Grooming bout durations were recorded to the nearest second, with the individual who initiated a grooming bout noted when possible. We recorded grooming given and received by focal subjects, as well as mutual grooming. We noted all instances of comforting or reassurance behavior, which included affiliative touches such as embracing, hand-holding, mouthing, genital-rubbing, gentle-touching, and mounting that occur frequently between mothers and offspring as well as other chimpanzees who share affiliative bonds (Goodall 1968).

Other behaviors that allowed individuals to maintain close proximity to one another or to maintain association while traveling, including who waited for, approached, left, and followed whom were noted *ad libitum*. Specifically, we defined focal subjects as approaching another individual if they came within 5 meters of them and no other chimpanzees and stopped. We scored focal subjects as receiving an approach if another individual did the same to him. If focal subjects or other individuals left this 5-meter space, focal subjects were designated as leaving or being left by another chimpanzee. If an individual "approached" focal subjects when they were traveling, or vice versa, we recorded our focal subject receiving a "follow" from this individual or that our focal subject "followed" this individual. Sometimes a focal chimpanzee stopped while traveling and looked back, occasionally standing bipedally or actually backtracking to reunite with another individual. When this occurred and the pair continued to travel in the original direction, we noted that the focal subject "waited" for the other chimpanzee. Alternatively, when a chimpanzee behaved this same way toward our focal subject, we scored this individual as having been the recipient of “waiting.” “Waiting” was also recorded if a focal chimpanzee finished feeding then sat below the tree where another individual was feeding and remained there until the other individual came down, even if the group traveled on. In this study, we classified these following and waiting behaviors as “travel vigilance.” These vigilance and waiting behaviors are typically shown by mothers to their dependent offspring (Pusey 1983) and by adults who have adopted orphans in other populations (e.g. Boesch et al. 2010). We also recorded instances where focal chimpanzees supported or received support from their siblings when they were targets of aggression. Aggression included displays, threats, chases, charges, and attacks involving contact aggression (Goodall 1968). We recorded acts of support when chimpanzees intervened in an ongoing dispute involving their sibling.

Ad libitum observations of social behavior involving non-focal subjects were also recorded. We report these *ad lib* observations because they provide information on a larger number of sibling pairs. Because focal and *ad libitum* data were collected differently, we do not combine them. We use *ad libitum* data to highlight unusual incidents that provide insights into the cognitive or emotional demands placed on older sibling caregivers.

Data Organization and Analysis

We investigated how maternal death influenced sibling relationships in three ways. First, we compared the behavior of the four chimpanzee sibling pairs before and after their mothers died. Second, we assessed how the behavior of individuals in the four orphaned pairs differed from the behavior of siblings whose mothers were alive. Third, we investigated the roles each sibling played in their relationship after being orphaned.

We calculated rates of association (percentage of total following episodes in association), proximity (percentage of total proximity scans in proximity), grooming (min/hr), reassurance, and travel vigilance between the 24 male subjects and their 27 younger, immature siblings. Calculations for travel vigilance included only younger siblings who moved independently of their mothers (n = 19 maternal siblings, 22 focal subjects, 24 pairs). For the denominators of the above values, we used the number of following episodes, scan samples, or focal observation hours recorded for a particular focal subject while his sibling was present in the community. For the four orphaned pairs, we calculated two rates for all the preceding measures, one rate for observations made before individuals lost their mothers and another rate after their mothers died. We used a series of generalized linear mixed model (GLMM) analyses to determine how maternal loss influenced the frequency with which: 1) a sibling pair associated; 2) maintained spatial proximity; 3) groomed; 4) reassured; and 5) displayed vigilance when traveling. In each analysis, one of the preceding variables was the outcome and the main predictor was whether or not a given sibling pair was orphaned. We included orphaned pairs twice in these analyses, once as orphans, and once as siblings with living mothers. Doing so allowed us to make three behavioral comparisons. We compared orphaned siblings before maternal death to siblings with living mothers, orphaned siblings before maternal death to themselves after maternal death, and orphaned siblings after maternal death to siblings with living mothers. To account for the fact that orphaned individuals and others (Table 6) appeared multiple times in this data set, we included the identities of focal subjects and maternal siblings as random intercept. We controlled for observation time by including it as an additional fixed effect. We controlled for age difference between siblings in a similar manner because we expected siblings close in age to interact more often than those separated by many years (cf. Mitani et al. 2002). All models assumed a negative binomial distribution.

We investigated how the dynamics of social relationships between recently orphaned chimpanzees changed after their mothers died. We determined each orphaned sibling's role in the relationship in two ways. We start by reporting how often each sibling initiated grooming and reassurance behavior and how equally grooming was given and received. Next, we determined who was responsible for maintaining spatial proximity. From our "approach" and "leave" data, we created two "proximity maintenance scores" for each of the recently orphaned sibling dyads. One score indicated the focal subject's responsibility for maintaining spatial proximity and the other indicated his sibling's score. Scores were calculated as:

Focal subject's proximity maintenance score = number of approaches to sibling – number of leaves from sibling

Sibling's proximity maintenance score = number of approaches received by focal – number of leaves received by focal

Positive proximity maintenance scores indicate that an individual approached their sibling more often than they left them. A score of zero indicated that they approached and left them an equal number of times, and a negative score indicated that an individual left their sibling more often than they approached them.

We used *ad libitum* observations to describe grooming, reassurance, and vigilance behavior involving all recently orphaned siblings shown in Table 1 as well as interactions between orphaned pairs Rosa and Rich Bergl, Wayne and Bach, and Rollins and Etta James. These observations included carrying during travel and defense against aggression from other individuals.

All data were entered into Microsoft Excel and organized and analyzed using the software R and the packages lme4 and lmerTest. Raw data files are included in our supplement. For our GLMM analysis, we employed z-score standardization to account for the different scales of the variables. We report coefficients and standard errors for main effect predictors. In the text we report the estimate effects of these predictors on outcome variables as odds or incidence rate ratios. We also report p-values to guide interpretation of results.

Results

Changes in sibling relationships following maternal death

Association & Proximity

Recently orphaned siblings altered their behavior in the immediate aftermath of losing their mothers. All orphaned pairs associated while their mothers were alive (mean ± SD = 58% ± 33% of the time), but they did so more often after losing their mothers (mean ± SD = 84% ± 18% of the time). The four orphaned pairs also associated more frequently (mean ± SD = 84% ± 18%) than other siblings whose mothers were alive (mean ± SD = 45% ± 24% of the time; Figure 7a). A GLMM analysis revealed that, when controlling for age difference, the time siblings spent in association increased by a factor of 6.5 after maternal loss (Table 8a). This pattern varied with the age of individuals in each pair. In three orphaned pairs both siblings were immature and traveling regularly with their mother before she died. In contrast, Buckner and his younger brother Holland did so less frequently when their mother was alive because Buckner was an adult and already traveling independently (Figure 7a).

All orphaned pairs maintained proximity to their younger siblings while their mothers were alive, with those close in age doing so most often (mean ± SD = 19% ± 16% of the time; Figure 7b). After their mothers died, orphans stayed near to each other more than they had previously (mean ± SD = 25% ± 10% of the time) and more so than did other pairs of siblings whose mothers were alive (mean ± SD = 9% ± 9% of the time). A GLMM analysis indicated that the frequency with which males in the four orphaned pairs maintained spatial proximity to their younger, immature siblings increased by a factor of 1.5 after maternal loss (Table 8b). This shift was less pronounced for orphans who were immature and frequently near each other and their mother when she was alive. After his mother died, 10-year-old Nelson actually spent less time in association with and in proximity to his younger sister, Amina, but Amina was still the individual with whom he maintained proximity most often. All four focal subjects had their younger sibling as their top proximity partner after being orphaned.

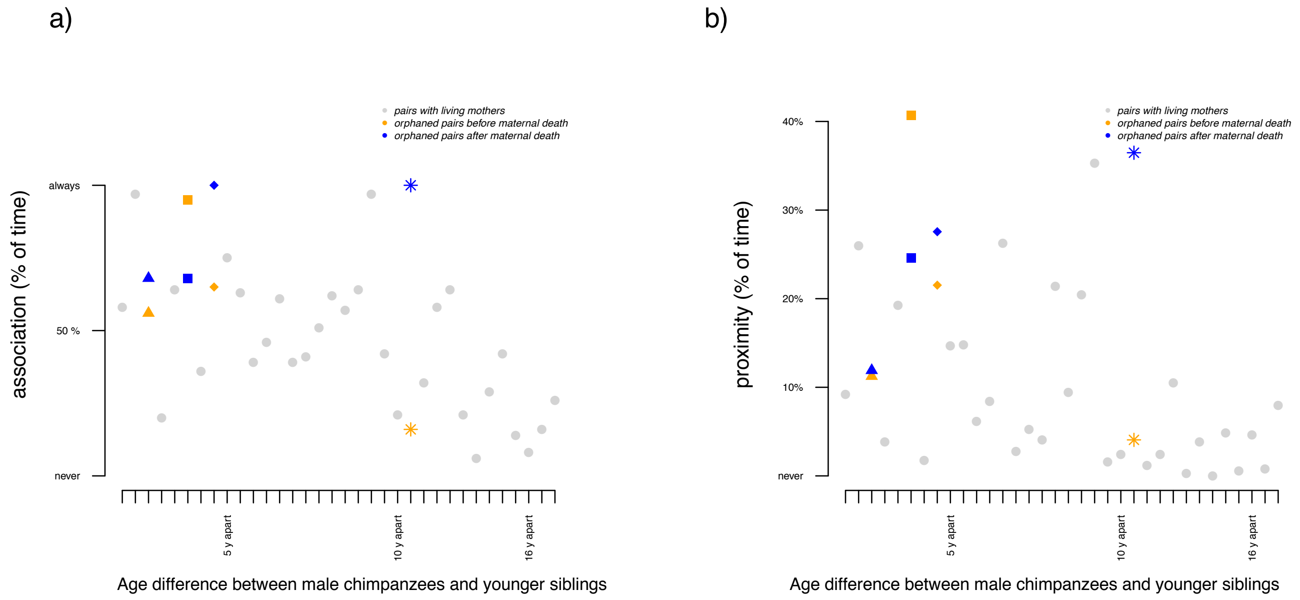


Figure 7. Rates of: a) association and b) proximity between focal males and their younger maternal siblings. Values for orphaned pairs Damien and Etta James (triangles), Nelson and Amina (squares), Yo Yo and Joya (diamonds) and Buckner and Holland (stars) are shown in orange before maternal death (9 months) and in blue after maternal death (8 months). Values for pairs whose mothers were alive (n = 30) are shown as gray circles.

Grooming

Chimpanzees in three of the four orphaned sibling pairs groomed each other while their mothers were alive (Figure 8a). The exception was Buckner and Holland. In contrast, all four pairs groomed after being orphaned, and did so at considerably higher rates (mean ± SD = 3.03 ± 2.15 min/hr) than they had when their mothers were alive (mean ± SD = 0.13 ± 0.09 min/hr; Figure 8a). All four orphaned focal males had his younger sibling as his top grooming partner. Grooming occurred between individuals in just 43% (13/30) of the sibling pairs whose mothers were alive. Still, they groomed each other at lower rates than did orphaned siblings (mean ± SD = 0.05 ± 0.09 min/hr). A GLMM analysis revealed that, when controlling for age difference, grooming between orphaned siblings increased by a factor of 7.9 after maternal loss (Table 8c).

Reassurance

Individuals in three of the four orphaned pairs displayed reassurance while their mothers were alive, but they did so rarely, just 6 times (mean ± SD = 1.5 ± 1.3 times per pair). After losing their mothers, all orphaned siblings reassured each other, and they did so frequently 31 times (means ± SD = 7.8 ± 1.5 times per pair; Figure 2b). Reassurance between orphans occurred considerably more often than between siblings whose mothers were alive. Individuals in just 33% (10/30) of these pairs displayed reassurance 29 times (means ± SDs = 0.96 ± 1.97 times per pair). A GLMM analysis showed that after maternal loss, the frequency with which chimpanzees reassured their younger siblings increased by a factor of 3.4 (Table 8d, Figure 8b).

Vigilance

Prior to maternal death, individuals in two orphaned pairs (50%) displayed vigilance while traveling, doing so only one time each (mean ± SD = 0.5 ± 0.58 times per pair). In contrast, individuals in all four orphaned pairs remained vigilant while traveling, doing so 84 times after losing their mothers (mean ± SD = 21 ± 10.1 times per pair; Figure 8c). Siblings whose mothers were alive looked out for each other while traveling together rarely. They did so only 12 times (mean ± SD = 0.6 ± 0.82 times per pair) in 45% of the pairs (9/20). A GLMM analysis showed that after maternal loss, the frequency with which chimpanzee siblings displayed vigilance while traveling increased by a factor of 14 (Table 8e).

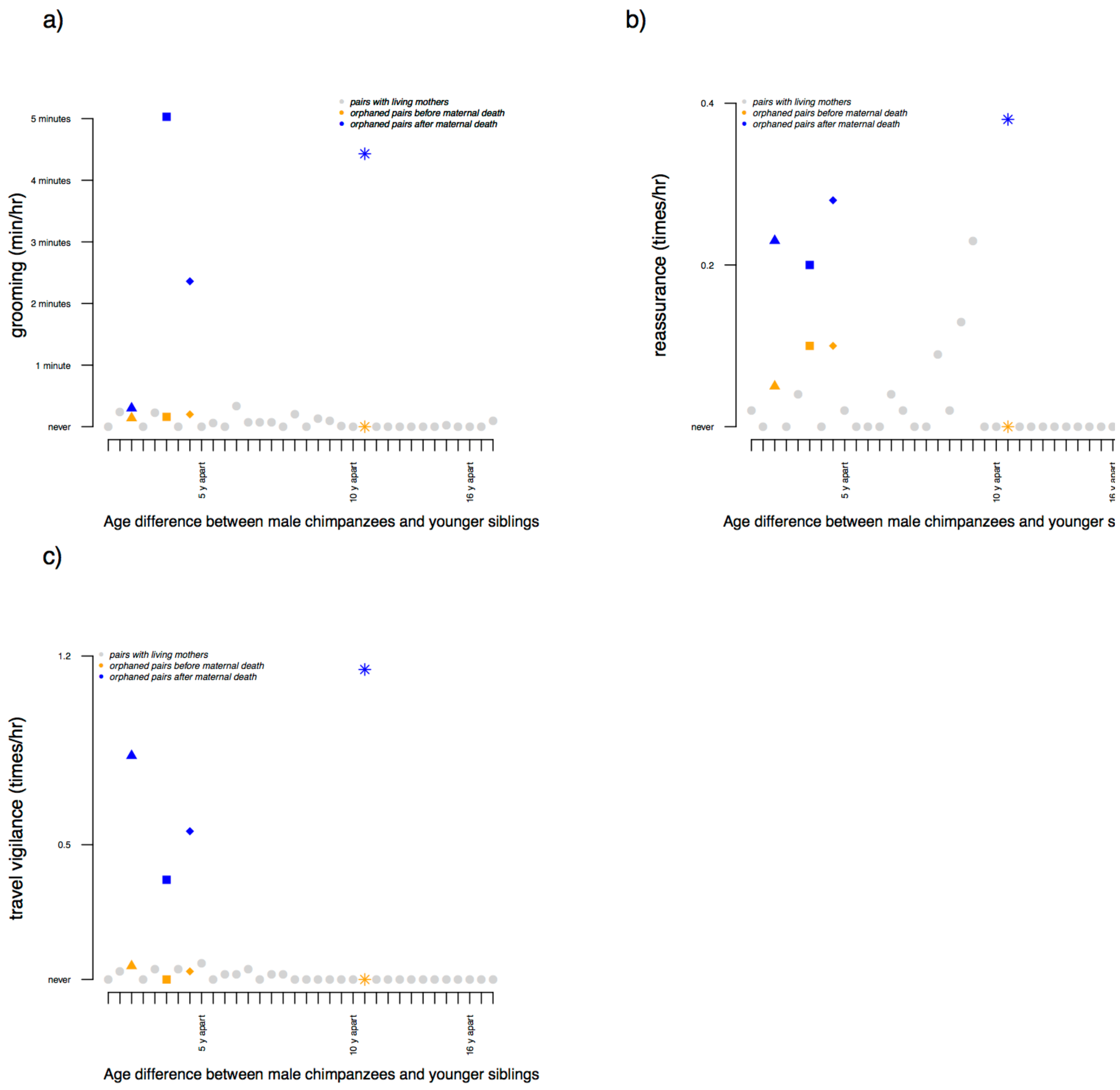


Figure 8. Rates of a) grooming; b) reassurance; and c) vigilance while traveling between focal males and their younger maternal siblings. Values for orphaned pairs Damien and Etta James (triangles), Nelson and Amina (squares), Yo Yo and Joya

(diamonds) and Buckner and Holland (stars) are shown in orange before maternal death (9 months) and in blue after maternal death (8 months). Values for pairs (n = 30) whose mothers were alive (n = 30) are shown as gray circles.

Table 8. Results of GLMM analyses where outcome variables are how often siblings in a pair associated, maintained spatial proximity, groomed, reassured each other, and displayed vigilance while traveling. Main effect predictors, their coefficients, standard errors, and summary statistics are shown. These models assumed a negative binomial distribution and included the identities of focal subjects and their siblings as random intercepts (*n* = 24 focal subjects, 27 siblings)

a) association

	Estimate	Std. Error	p-value
intercept	18.67	1.45	
age difference	-7.09	2.26	0.004
observation time	6.62	2.15	0.005
orphan status	6.05	1.79	0.004

b) proximity

	Estimate	Std. Error	p-value
intercept	2.89	0.19	
age difference	-0.79	0.28	0.005
observation time	0.46	0.29	0.113
orphan status	0.42	0.19	0.027

c) grooming

	Estimate	Std. Error	p-value
intercept	0	0.48	
age difference	-1.89	0.55	0.001
observation time	0.78	0.54	0.148

orphan status	2.07	0.19	<0.001

d) reassurance

	Estimate	Std. Error	p-value
intercept	-0.49	0.44	
age difference	-0.63	0.74	0.40
observation time	0.36	0.63	0.57
orphan status	1.22	0.29	<0.001

e) travel vigilance (n = 24 pairs)

	Estimate	Std. Error	p-value
intercept	-0.11	0.27	
age difference	-0.28	0.6	0.641
observation time	0.34	0.55	0.532
orphan status	2.64	0.31	<0.001

Dynamics of sibling relationships following maternal death

We examined how maternal death influenced the dynamics of sibling relationships. Specifically, we investigated who was responsible for initiating grooming, reassurance, and proximity. We recorded 327 grooming bouts between individuals in the four orphaned pairs. Sixty-seven of these bouts had a clear initiator, with younger siblings initiating grooming the majority of the time (64% = 43/67). Grooming, once it began, was not equitable between all dyads, but no clear pattern based on age or age difference emerged.

We recorded reassurance between siblings in the four orphaned pairs 31 times. All but four of these (87%) were initiated by younger chimpanzees and typically involved them approaching and then touching their older sibling with their hand, arm, mouth, or genitals. Two times the older chimpanzee made the initial approach and touched its younger sibling when it screamed or cried. Two other times both siblings approached each other simultaneously. This behavior occurred when both seemed frightened due to adult males displaying nearby or because calls of neighboring chimpanzees were heard.

Younger siblings were responsible for maintaining spatial proximity to their older siblings (Figure 9). Proximity maintenance scores indicated that older siblings were more likely to “leave” their younger sibling than vice versa. These scores do not explain the situation completely because qualitative observations suggest that older siblings were still concerned about the welfare of the younger orphan. Older siblings left their younger siblings, but they often did so at the start of travel. During travel, they were followed by their younger siblings more often than vice versa. While traveling, however, older siblings often waited and looked back for their younger sibling, typically without the latter crying or soliciting the attention of the former. Thus, by waiting, older siblings appeared to be maintaining associations with and keeping a watchful eye on their orphaned younger siblings.

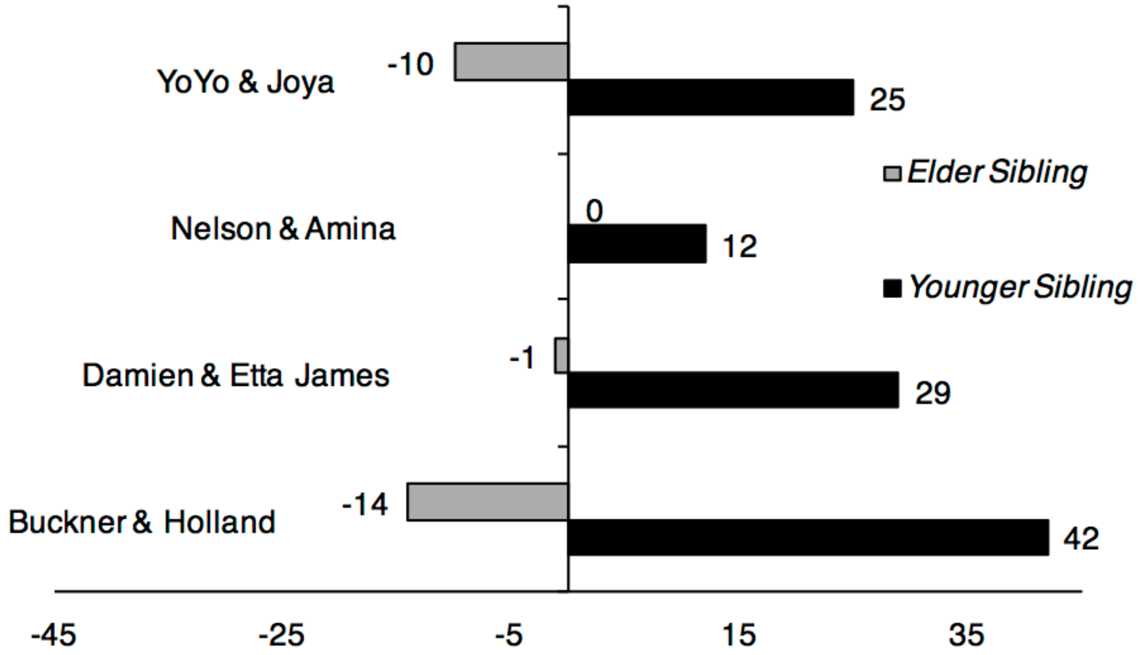


Figure 9. Proximity maintenance scores between four orphaned focal subjects and their younger siblings. Positive proximity maintenance scores indicate that an individual initiated and maintained proximity while negative scores indicate that an individual tended to terminate proximity. For each dyad, the proximity score of the older sibling is shown in gray and that of the younger sibling in black. See text for further explanation.

Ad libitum observations of changes in sibling behavior following maternal death

Ad libitum observations of recently orphaned chimpanzees under age 12 reinforced patterns that emerged from the preceding analyses of focal observation data. Orphaned siblings associated and maintained proximity. Orphaned siblings groomed each other, and younger siblings groomed older siblings more often than the reverse. Similarly, older siblings reassured their younger orphaned siblings, with the latter typically initiating such behavior. Young orphaned chimpanzees followed their older siblings. Finally, older siblings waited for their younger siblings, sometimes stopping and looking back for them while traveling.

Aggression toward immature orphans occurred rarely. We therefore have few observations of older siblings defending younger chimpanzees. Anecdotally, older siblings remained attentive to their younger siblings and helped them when they received aggression from others. On some occasions, older siblings looked toward a scream and approached the source of the call. A few times, they intervened, directing aggression to the chimpanzee who had caused their younger sibling to scream. For example, an adolescent male, Billy Bragg (12 y old), displayed at orphan Holland (7 y old) when Holland attempted to climb and feed in a small *Uvariopsis* tree. Holland's brother, Buckner (17 y old) then leapt to this tree from a nearby one, became piloerect, and charged Billy Bragg, who stopped displaying. Holland was then able to feed. Chimpanzees with mothers also occasionally attended to the screams of their siblings in ways similar to those described here. Still, such behavior, much like that shown during travel, intensified and became more frequent between siblings whose mothers had recently died.

In addition to grooming, reassurance, traveling, and defense, an adolescent female Rosa (11 y), carried her infant brother, Rich Bergl (4.5 y) dorsally while traveling in the month following their mother's death. Once, this carrying was prompted by Rich Bergl. As he cried, he put his arms around Rosa's back and then jumped on. At first, Rosa pushed him off, but later, as the group traveled quickly Rosa paused and gestured for him to "climb on" (cf. Hobaiter & Byrne 2014). Rich Bergl continued to ride as Rosa moved a long distance. Other than Rich Bergl, who was the youngest surviving orphan, most orphans were no longer consistently riding on their mother's back when she died. Non-orphans also occasionally carried their maternal siblings and unrelated infants while traveling. Unlike the case above, carrying was not initiated by crying on the part of the younger sibling and did not occur during concerted long-distance group travel. Rather, dorsal and ventral carrying between non-orphans was often initiated by older siblings, who picked up younger ones, sometimes during play, and placed them on their backs or chests, or by the younger sibling playfully hopping onto the older sibling's back (e.g. Goodall 1968).

Some anecdotal observations may reveal emotions that emerge in sibling relationships after maternal death for both older and younger siblings. For example, adolescent chimpanzees occasionally whimper or cry when they fall behind the group or another individual such as their mother. Twice, however, adolescent orphans (Rosa, 11, and Nelson, 10), cried as they searched for their younger siblings. In both cases, the older orphans cried, ran around frantically among a party of chimpanzees, and stopped crying after finding their siblings. After maternal death, young orphans sought frequent reassurance from their older siblings, but they did so in a qualitatively different way. For example, 7-year-old orphan Holland seemed to seek almost constant physical contact with his 17-year-old brother, Buckner. Holland would regularly sit so that his shoulder touched Buckner’s and often, while Buckner sat upright, Holland pressed his own back into Buckner’s chest or shoulder, occasionally whimpering (Figure 10). This continued for at least 8 months after their mother’s death.

Figure 10. Young orphan, Holland (right), rests with his arm pressed against his adult brother's (left) shoulder. Recent orphans often sought comfort from older siblings in this manner. Photo by Kevin Lee.

Additional observations suggest that older siblings showed heightened vigilance in times of danger. Eight months after Kanawa's death in 2017, her offspring Rollins (31 y) Damien (11 y), Etta James (6 y) and an unrelated adolescent male, Billy Bragg (12 y), traveled into the territory of neighboring chimpanzees. Being in this area, especially in small numbers or alone, is dangerous for chimpanzees (Wilson & Wrangham 2003; Mitani et al. 2010). While there, the chimpanzees in this group were extremely quiet and moved carefully checking trees for fruit. None of the males stopped to feed in any of the trees, but Etta did on two occasions, and both times, Rollins sat below the tree and waited for her to start and finish feeding and come back to the ground before moving on. He also regularly looked back for both of his siblings while they continued to move in the territory of their neighbors. As they returned to the Ngogo territory and met other community members, Rollins moved farther ahead of Damien and Etta and no longer waited below trees where they stopped to feed unless he too, fed there.

Finally, some siblings altered their behavior in similar ways when their mothers were still alive and temporarily absent or on a sexual consortship (Tutin 1979). Consorting behavior by adult female Kanawa, who later died, allowed us to observe some of these dynamics. Prior to her death, Kanawa went on two consortships that lasted up to 2.5 months, one in 2015 and another in 2016. During these episodes Kanawa left both Etta James and Damien behind. The first time Kanawa left, Rollins was 29 years old, Damien was nine years old and Etta James was four years old. One time Rollins and two other adult males crossed paths with a group of adult females and their offspring and Damien and Etta James. The adults in both parties continued traveling in opposite directions but Damien stopped and turned around to follow Rollins instead of the group of females. Etta, however, had already gone ahead with the adult females and was out of view. As Rollins kept traveling, Damien paused, stood up on two legs, and looked back. He continued to do this, while moving short distances toward his older brother. Finally, Etta appeared alone, whimpering, and Damien, still standing bipedally, looked over to her. She began screaming and ran to him. Damien embraced her and she fell quiet. After this, he let go and began running quickly to catch up to Rollins with Etta following. The siblings remained together until late in the evening. When Kanawa returned, Damien no longer waited or looked back for Etta. Importantly, Damien appeared to keep a watchful eye on Etta in the absence of her seeking his attention.

Discussion

After losing their mothers, recently orphaned chimpanzees intensified their social interactions with at least one of their maternal siblings if they had one. If both orphans were close in age and immature (<12 years) and had thus almost always been together with their mother prior to her death, they continued to do so after she died and interacted even more frequently. In addition, mature chimpanzees, who had interacted only occasionally with their younger siblings prior to losing their mother, now had them in almost constant company with younger siblings initiating most of the contact. For all adolescent and young adult male focal subjects, their younger immature orphaned sibling became the individual with whom they most often groomed and spent time in close spatial proximity. Furthermore, the rate at which these orphaned siblings interacted was higher than that of siblings whose mothers were alive.

Social interactions between recently orphaned siblings included behaviors that were common, but less frequent between non-orphaned siblings such as maintaining association and proximity and grooming, but also some behaviors that were infrequent or absent between siblings with living mothers. The behaviors that emerged or became regular occurrences only after maternal loss, included comforting reassurance acts such as embraces, hand-holding, and mouthing suggested to be important for the emotional development of orphans (Clay & deWaal 2013), as well as extreme vigilance demonstrated during group travel through following, waiting for, and looking for each other. Older orphans also occasionally carried their younger siblings dorsally during travel and defended them against aggression from other chimpanzees when they screamed. Thus, after losing their mother, older siblings appeared to take on a new type of role in the lives of their younger siblings (cf. Hobaiter et al. 2014).

Virtually all social behavior between orphaned siblings was initiated by younger siblings, indicating the active role they played in the relationships. Younger siblings typically started grooming and groomed their older sibling more than they received grooming from them though this was not the case for all pairs. They were almost always the ones to seek reassurance, approach, and maintain spatial proximity, and follow their older siblings during travel. Still, it seemed important to older siblings that this spatial proximity was maintained, especially during travel. While their younger siblings approached and followed, older siblings often waited for them to catch up and finish feeding. Older siblings also looked for their younger brothers and sisters before traveling, sometimes backtracking or standing bipedally to extend their view. This leaving and waiting pattern mirrors that shown by mothers to their dependent offspring; mothers typically leave their juvenile offspring when they begin to travel, but wait for them to follow (Pusey 1983).

Certain behaviors revealed the potential cognitive and emotional demands of caregiving. Older siblings seemed to offer maternal-like care when mothers were absent. For example, adolescent male Damien took care of his younger sister Etta James when their mother, Kanawa, was on consort, but not after she returned. He then resumed this role after Kanawa died. Serving as a caregiver was flexible, and did not necessarily depend on his sister soliciting care, but instead contingent on maternal presence or absence. This flexible, temporary adoptive behavior when a mother is sick or injured has been described in other chimpanzee groups (Uehara & Nyundo 1983; Pruetz 2011). Sibling caretakers also showed heightened vigilance, looking back for siblings and waiting for them to catch up or finish feeding in potentially dangerous situations, such as travel outside of the territory.

This flexible waiting behavior in chimpanzees is of particular interest, because small-bodied juvenile chimpanzees who are not carried during travel may pose a ranging cost to their adopters. Mothers with dependent juveniles have shorter day ranges than mothers with infants who still cling (Pontzer & Wrangham 2006). Pontzer and Wrangham (2006) suggest that this may occur because when small-bodied juvenile offspring cannot keep up with traveling parties, mothers choose to leave parties rather than "abandon" their offspring. Male chimpanzees who adopt their juvenile siblings may be faced with similar choices. For instance, Rollins "abandoned" his trailing 6-year-old sister in a large party with other group members, but was unwilling to do so while traveling with her outside of the territory when he was the only adult. In other chimpanzee groups, both maternal siblings and maternally unrelated adopters are similarly unwilling to leave lagging adoptees behind; instead, they wait for and carry them (Goodall 1983; Uehara & Nyundo 1983; Boesch et al. 2010; Pruetz 2011; Hobaiter et al. 2014). Waiting for, retrieving, and carrying adoptees before group movement is also common in other species whose infants are typically carried by mothers (e.g baboons: Hamilton 1982; ring-tailed lemurs: Gould 2000).

Caring for younger siblings appeared to have emotional importance, and perhaps place a toll on older siblings. Specifically, separation from their younger charges occasionally caused older siblings visible distress. They cried until they found their younger siblings. Importantly, crying when separated from a specific individual, while relatively common for infant and juvenile chimpanzees, was rare in the older adolescents who showed this behavior. It is possible that having a sibling, even one who requires considerable care, might buffer an older sibling's grief. Grief and depression, for both humans and nonhuman animals, may sometimes be buffered by the strengthening of existing relationships and the formation of new ones (Engh et al. 2005; Stroebe et al. 2005; Dopp & Cain 2012). Here, studies of the physiology of these individuals before and after their mothers died would provide important insights into how sibling adoption might affect older siblings. For example, adoption is likely to stress individuals who take on the burden of caring for others, and this might be revealed by comparing the cortisol levels of individuals who adopt others before and after doing so. Other costs incurred by older siblings, who start to care for their younger siblings, constitute an important issue that will require future study. These costs include less time to allocate to feeding and other social relationships that will impact fitness.

Additional research will also be required to document the long-term benefits that older siblings provide younger orphans. Adoption increases the probability that orphans will survive over the short term in chimpanzees (Goodall 1983; Boesch et al. 2010; Hobaiter et al. 2014). However, in several species, even when orphans survive, they can experience decrements in growth, reproduction, and longevity and suffer negative impacts on health, social status, and emotional development (e.g. Asian elephants: Ladenphera et al. 2016; baboons: Tung et al. 2016; red deer: Andres et al. 2013, humans: Cerel et al. 2006, chimpanzees: Nakamura et al. 2014; Walker et al .2018; Samuni et al. 2020; Stanton et al. 2020; bonobos: Clay & deWaal 2013). How sibling adoption buffers orphans against these deleterious consequences in chimpanzees is currently unknown, but it appears to have long-term benefits in some other species (Engh et al. 2009).

In sum, the observations presented in this paper add to a body of literature on the importance of kin relationships and adoptive behavior in chimpanzees (for review, see: Hobaiter et al. 2014) and other mammals (e.g. elephants: Lee 1987; baboons: Engh et al. 2009). They also provide insights into the flexibility of caregiving behaviors by males, who, in many primate species, in addition to chimpanzees and baboons described here, adopt infants (Pope 1998; Struhsaker 2008; Gould 2000). Taken together, these findings contribute to our understanding of the evolution of alloparental behavior, an integral feature and part of our own species' behavior that influences offspring survival (Hrdy 2009).

Chapter 4

Adolescent and Young Adult Male Chimpanzees Form Affiliative, Yet Aggressive Relationships with Females

Note on Publication

Chapter 4 is published in the *Journal of Human Evolution* as a research article, co-authored by my dissertation chair, Dr. John Mitani (Reddy & Mitani 2020).

Abstract

Primates frequently form affiliative relationships that have important fitness consequences. Affiliative relationships between unrelated males and females are ubiquitous in humans, but are not widely reported in our closest living relatives, chimpanzees *(Pan troglodytes*). Instead, adult male chimpanzees are extremely aggressive to females using this to coerce females to mate with them. Adolescent male chimpanzees are physically and socially immature and unable to use aggression toward females in the same way as adult males. Instead, adolescent males might build affiliative relationships with females as an alternative tactic to increase their chances of mating and reproducing. To investigate this possibility, we recorded social interactions between 20 adolescent and 10 young adult males and 78 adult female chimpanzees over 2 years at Ngogo in Kibale National Park, Uganda. Analyses using grooming and proximity as assays revealed that adolescent and young adult males formed differentiated, affiliative relationships with females. These relationships were as strong as the bonds young males formed with maternal kin and unrelated males and increased in strength and number as males aged and started to dominate females. Male-female relationships extended outside the immediate context of mating. Although males affiliated slightly more often with females when they were cycling, they also did so when females were pregnant and nursing young infants. Males and females who formed bonds reassured each other, looked back and waited for each other while

traveling, and groomed more equitably than did other male-female pairs, even after the time they spent together in association and the female's reproductive state were taken into account. Despite the affiliative nature of these relationships, adolescent and young adult males selectively targeted their female partners for aggression. These findings provide new insights into the evolution of social bonds between human females and males, which can involve both affiliation and coercive violence.

Introduction

Primates that live in large groups form differentiated social bonds from which they derive various benefits (Cheney et al., 1986; Seyfarth & Cheney, 2012). For example, female baboons, who remain in their natal communities for life, form strong and long-lasting relationships with their maternal kin (Silk et al., 2010). These relationships have important short-term physiological and long-term fitness consequences. Affiliative contact can alleviate stress, and female baboons with secure and enduring relationships raise more surviving infants and live longer lives than do individuals who are unable to forge similar bonds (Cheney & Seyfarth, 2009; Silk et al., 2003; 2009; 2010; Beehner et al., 2005). In some primate species, unrelated males and females also form bonds or "friendships" outside the context of mating. These relationships are characterized by frequent grooming and spatial proximity (e.g. yellow baboons, *Papio cynocephalus*: Nguyen et al., 2009; olive baboons, *Papio anubis*, Smuts, 1985; Japanese macaques, *Macaca fuscata*: Takahata, 1982; Assamese macaques, *Macaca assamensis*: Haunhorst et al., 2016). Males that develop these friendships engage in behaviors that have potential fitness consequences. For example, male chacma baboons (*Papio ursinus)* attend to threats to their friends' infants that are likely to be their own and are vulnerable to infanticide (Palombit et al., 1997; Palombit, 2009).

Our closest living relatives, chimpanzees (*Pan troglodytes*), also form enduring social bonds with conspecifics. They live together in “unit groups” or communities that consist of 20 to 200 individuals that fission and fuse to form temporary subgroups or “parties” that vary in size and composition (Nishida, 1968; Goodall, 1986). Strongly bonded chimpanzees often associate and travel in the same parties (Nishida, 1968; Goodall, 1986) They also maintain close spatial proximity, groom each other often and equitably, reassure one another, provide coalitionary support, and cooperate to defend their territory (Goodall, 1986; Watts & Mitani, 2002; Mitani, 2009; Langergraber et al., 2017). Bonds between adult male and maternally related chimpanzees are especially notable and strong, as males remain in their natal community with their mothers and adult brothers for life (Goodall, 1986; Hayaki, 1988; Mitani et al., 2000; Langergraber et al., 2007; Gilby & Wrangham, 2008; Mitani, 2009; Machanda et al., 2013). Unrelated males and females spend time together in the same parties when females are not cycling, but they have not been described to develop highly affiliative, conspicuous social relationships outside the immediate context of mating (Tutin, 1979; Goodall, 1986; Takahata, 1990, Matsumoto-Oda, 2002; Lehmann & Boesch, 2005; Gomes & Boesch, 2009; Langergraber et al., 2013; Machanda et al., 2013; Kaburu et al., 2015). Instead, adult males are extremely aggressive to both estrous and anestrous females (Goodall, 1986; Muller et al., 2007, 2011; Feldblum et al., 2014; Kaburu et al., 2015). Some of this aggression represents sexual coercion. Males mate and sire more offspring with females to whom they direct the most aggression (Goodall, 1986; Smuts & Smuts, 1993; Muller et al., 2007, 2011; Feldblum et al., 2014; Kaburu et al., 2015; but see: Stumpf & Boesch, 2010) doing so selectively to specific females (Muller et al., 2011; Feldblum et al., 2014).

The prominent role sexual coercion plays in adult male chimpanzee behavior does not preclude the possibility that male and female chimpanzees form social bonds. Affiliation with females might be especially important for adolescent male chimpanzees because they can neither successfully coerce females nor challenge other males. Male chimpanzees fight for dominance status (Bygott, 1974; Goodall, 1986), and high-ranking males sire more offspring than low-ranking males (Constable et al., 2001; Boesch et al., 2006; Wroblewski et al., 2009; Newton-Fisher et al., 2010). During adolescence male chimpanzees are still physically and socially immature and thus low-ranking and subordinate to adult males and females (Goodall, 1986; Pusey, 1990; Hayaki, 1988; Takahata, 1990; Nishida, 2011; Langergraber et al., 2013). At the end of adolescence (~16 y), males reach adult size and dominate all females in their community, but they may be 20 years old before they start to rise in the male dominance hierarchy (Goodall, 1986; Kawanaka, 1993; Watts, 2018). Because they cannot fully dominate females, adolescent males may be unable to use aggression to sexually coerce them, raising the possibility that they might rely on other tactics, including forming affiliative bonds to increase their chances of mating. These considerations suggest that if male chimpanzees develop affiliative social relationships with females, they are likely to do so during adolescence.

In this paper we investigate affiliative and aggressive behavior between adolescent and young adult male chimpanzees and unrelated females. We start by testing the hypothesis that adolescent and young adult males affiliate with unrelated females. We do so by comparing grooming and proximity interactions between them with those displayed between adolescent and young adult males and all other mature individuals, including pairs that have been previously shown to groom and maintain proximity often. The latter include other males and maternal kin. These analyses reveal that some male-female pairs affiliate frequently and that the bonds they form cannot be entirely explained by variation in the reproductive state of females. We further characterize the affiliative nature of these relationships by examining whether these dyads also engage in additional prosocial behaviors, including reassurance and coordinated travel. We then turn to an analysis of male aggression toward females by determining when this well-known behavior displayed by adults emerges and whether it is a component of affiliative relationships. Specifically, we ask whether it develops early during adolescence when males are unable to dominate all adult females or later in young adulthood when males outrank all females. We conclude with an investigation of how affiliation, aggression, and dominance rank relationships between adolescent and young adult males and unrelated females change with male age.

Methods

Study Site & Subjects

Research took place at Ngogo in Kibale National Park, Uganda, a mid-altitude rainforest (Strushaker, 1997). Members of the Ngogo chimpanzee community occupy a territory of approximately 35 square kilometers (Mitani et al., 2010). Study of the Ngogo chimpanzees was initiated by J.M. and David Watts in 1995. Male chimpanzees have been followed continuously since that time, and females have been regularly followed since 2004. The ages of natal individuals younger than 20 years old are known within one day to one year, while the ages of older individuals are estimated based on their genetic relationships to other individuals, physical appearance, and behavior (Wood et al., 2017). Immigrant females are estimated to be 13 years old when they enter the community (Wood et al., 2017*)*. During this study, the Ngogo community ranged between 181 – 217 chimpanzees, including 136 sexually mature individuals of both sexes. We considered females to be mature if they had begun to exhibit sexual swellings (ca. 11 years old). We considered males to be mature if their testicles had descended and were visible (between 8 – 10 years old).

Twenty adolescent (9 – 15 years) and 10 young adult male chimpanzees (16 – 20 years) were the focal subjects of this study and followed by R.R. over 17 months during June – August 2015 and June 2016 – August 2017. Each subject was observed for at least 25 hours (mean ± SD = 47.6 ± 6.6 hours per focal animal; range: 25 – 61 hours) and on at least 19 different days (mean ± SD = 33.8 ± 6.2 days per focal animal; range: 19 – 47 days). During focal observation sessions, R.R. recorded behavioral interactions between adolescent and young adult males and other community members, including 57 mature males and 78 mature females. These individuals composed 59 dyads that included focal subjects and their mature maternal kin (mothers and maternal siblings of both sexes), 1672 dyads involving focal subjects and mature males who were not their maternal brothers, and 2276 dyads comprising focal subjects and mature females who were not their mothers or maternal sisters. Sixty-two of these mature females were parous or gave birth for the first time during the study, while 16 were nulliparas.

Behavioral Observations

Efforts were made to locate and observe male subjects every month and for most months, each male was followed multiple times. Focal observation sessions typically lasted 3 hours. After following one focal chimpanzee for 3 hours, R.R. switched to a new focal subject, choosing one whom she had observed the least or had not followed that month. If no other focal subject was in the current party, she remained with her current subject for 5 hours before leaving to search for a different chimpanzee. In rare instances when R.R. did not know where other chimpanzees might be, the current focal individual was followed for more than 5 hours. During focal following sessions, R.R. recorded chimpanzees of all age and sex classes who were in association with focal subjects at one-hour intervals. Chimpanzees observed in the same party as focal subjects during the hour-long focal following episodes were defined to be in association (*cf*. Chapman et al., 1994). Individuals within 5 meters of focal subjects were recorded every 10 minutes, and the amount of time focal subjects gave and received grooming was noted to the nearest second *ad libitum*.

During focal following episodes, R.R. recorded *ad libitum* additional affiliative behaviors, specifically reassurance and vigilance during travel between focal males and other individuals, including mature females. Reassurance behaviors included gentle touches, mouthing, kissing, hand-holding, embracing, genital-rubbing, and mounting between pairs (van Lawick-Goodall, 1968). Reassurance often occurred between focal males and females in tense or frightening situations, such as when greeting each other after a long separation while aggression occurred around them. Reassurance also took place when individuals were relaxed and resting together, e.g. "affectionate behavior" (van Lawick-Goodall, 1968, p. 244). Travel vigilance included following, checking, and waiting behaviors that ensure individuals remain together. These behaviors are displayed by mothers to their dependent offspring (Pusey 1983) and by mature chimpanzees to adoptees (e.g., Boesch et al. 2010; Reddy and Mitani 2019). Specifically, we defined focal subjects as approaching another individual if they came within 5 m of that individual and no other chimpanzees and stopped. We scored a focal subject as receiving an approach if another individual did the same to him. If an individual “approached” focal subjects when they were traveling or vice versa, we recorded our focal subject receiving a “follow” from this individual or that our focal subject “followed” this individual. Sometimes a focal chimpanzee stopped while traveling and looked back, occasionally standing bipedally or backtracking to reunite with another individual. When this occurred and the pair continued to travel in the original direction, we noted that the focal subject “waited” for the other chimpanzee. Alternatively, when a chimpanzee behaved this same way toward our focal subject, we scored this individual as having been the recipient of “waiting.” “Waiting” was also recorded if a focal chimpanzee finished feeding then sat below the tree where another individual was feeding and remained there until the other individual came down, even if the group traveled on.

We recorded aggression directed by focal males to mature females. We quantified male aggression as the number of times males threatened, displayed, charged, chased, hit, kicked, and bit females (van Lawick-Goodall, 1968; Muller et al., 2007). We also recorded all pant grunts, calls given by low-ranking chimpanzees to higher-ranking individuals (Bygott 1974), made by our focal subjects and directed to them.

Female reproductive state

We noted daily whether females in association with focal subjects had full sexual swellings, but we did not collect hormonal samples from females to ascertain whether conception was possible during these times. Instead, we used infant birth dates to determine when females were able to conceive retrospectively. We considered females to be non-cycling if they were pregnant (estimated gestation period = 243 days), had yet to exhibit sexual swellings following a birth, or exhibited swellings but were nursing an infant which was less than two years old (Emery Thompson, 2013).

Analyses

Defining affiliative relationships

To quantify the strength of affiliative relationships between focal males and other chimpanzees, we used the frequency with which pairs groomed and maintained spatial proximity across the study period to create an affiliation index adapted from Silk and colleagues (2006a):

$$\frac{\left(\frac{\mathrm{G}ab}{\mu\mathrm{G}} + \frac{\mathrm{P}ab}{\mu\mathrm{P}}\right)}{2}$$

The numerator of the first term denotes the rate (minutes per focal observations) male *a* groomed with individual *b*; its denominator indicates the mean grooming rate recorded during the study between all mature dyads in the community. The numerator of the second term denotes the rate (proportion of scans) male *a* was in proximity to individual *b,* and its denominator indicates the mean proximity rate between mature dyads in the community.

We examined the distribution of affiliation indices for all 4,007 possible pairs involving our 30 adolescent and young adult male subjects and other mature individuals in the community. Following the precedent established by previous studies (e.g., Silk et al. 2006a), we defined pairs who fell in the top 10 % as strongly bonded. We report how many times focal males formed strong bonds with maternal kin, defined as mothers and maternal siblings, and with mature males and females who were not maternal relatives. We also report how often unrelated mature females appeared in the top five strongest bonds for each focal male. While we used the 10% cutoff to differentiate strongly bonded pairs from those without strong bonds, we employed the affiliation index as a continuous variable in all of our subsequent analyses.

Effect of female reproductive state on male – female relationships

Male chimpanzees show a keen interest in female chimpanzees when they are cycling irrespective of whether they possess a full sexual swelling (Tutin 1979; Feldblum et al. 2014). For example, males target non-swollen, cycling females for aggression, and this affects their likelihood of siring infants with them (Feldblum et al. 2014).

Affiliative bonds between males and females may simply reflect a male's interest in immediate mating opportunities. To exclude this possibility, we examined pairs of males and females who fell in the top 10% of the affiliation index distribution. For each male we tabulated the amount of time that he spent in spatial proximity and grooming with each female in two reproductive states, either cycling or non-cycling. Some females cycled during the entire study, others remained anestrus throughout, while some were observed in both reproductive states. We then conducted two generalized linear mixed model (GLMM) analyses. In the first, the outcome variable was proximity between pairs, assessed by the number of scans in proximity. In the second, the outcome variable was grooming evaluated by the number of minutes spent grooming. In both models the main predictor was whether or not the female was cycling. We controlled for observation time by including it as a fixed effect. Observation time was calculated for each pair as the number of hours focal males were observed while a particular female was present in the community and either cycling or non-cycling. Because we wanted to determine whether male affiliation with females reflected an interest in the female herself and not only mating opportunities created by her reproductive state, we calculated two observation time variables for each male-female pair, one that included the number of hours we observed the male while the female was cycling ("cycling observation time") and one that included the number of hours we observed the male while the female was not cycling ("non-cycling observation time").

Finally, to account for some pairs appearing more than once in these analyses we included male and female identities as random intercepts. Both proximity and grooming models assumed a negative binomial distribution.

Characterizing the nature and quality of relationships and controlling potential confounds

To ascertain whether the relationships between males and mature females who had high affiliation indices differed from those between pairs with low affiliation indices, we compared the number of times both types of pairs reassured each other and displayed vigilance during travel. We conducted two GLMMs that assumed a negative binomial distribution, where the main predictor variable was the affiliation index of a male -female pair and outcome variables were: 1) the number of times individuals reassured each other and 2) the number of times they displayed vigilance while traveling. One reason pairs with high affiliation indices might engage in the preceding behaviors is because they associate frequently and consequently have more opportunities to interact. By being together male and female chimpanzees are already "choosing" to interact, but we wanted to determine how often reassurance and vigilance could be explained as part of an affiliative relationship *per se* and not by association alone. We therefore controlled for association in the preceding analyses by including it as an additional fixed effect in both models. We controlled for observation time in the same manner, calculating this for each pair as the number of hours we observed a focal male while a particular female was present in the community and either cycling or non-cycling. Male and female identity were included as random intercepts in both models.

Chimpanzee grooming relationships are typically unbalanced, with high-ranking individuals receiving more grooming than low-ranking individuals even in dyads that groom often (Watts, 2000; Sandel et al., 2020). Adolescent males, who are low-ranking, frequently groom others without receiving any grooming in return (Sandel et al., 2020). In contrast, adult males who form especially strong and enduring bonds groom each other more equitably than do pairs who fail to forge similar ties (Mitani, 2009). To investigate whether affiliation between adolescent and young adult males and females affected the quality of their relationships, we computed a grooming equality index between focal males and other chimpanzees. This index produces values between 0 and 1, where 0 indicates an entirely skewed grooming relationship and 1 indicates a perfectly balanced one (Silk et al., 2006b; Mitani 2009). The grooming index is computed as follows:

$$1 - \left| \frac{\mathrm{ga} \rightarrow \mathrm{gb}}{\mathrm{ga} \Leftrightarrow \mathrm{gb}} - \frac{\mathrm{gb} \rightarrow \mathrm{ga}}{\mathrm{ga} \Leftrightarrow \mathrm{gb}} \right|$$

where $g_a \rightarrow g_b$ is the amount of time (in minutes) male a groomed individual b during focal observations of individual a, $g_b \rightarrow g_a$ is the amount of time that male a received grooming from individual b during focal observations of individual a, and $g_a \Leftrightarrow g_b$ is the total amount of time male a and individual b groomed during focal observations of individual a. We excluded instances that individuals spent mutually grooming for this measure.

We compared grooming equality indices between males and females who had high affiliation indices to those between males and females who had low affiliation indices to assess whether the quality of their social bonds differed. We also conducted a GLMM analysis that assumed a negative binomial distribution where the outcome variable was the grooming equality index between a male-female pair and the main predictor variable was the pair's affiliation index. As in models examining reassurance and vigilance behavior, we accounted for the amount of time males and females spent in association and for cycling and non-cycling observation time by including these variables as additional main effects. The identities of males and females were included as random intercepts.

Male aggression toward females

We examined whether affiliative relationships affected male aggression toward females. We did so by comparing the number of times males directed aggression to females with whom they formed strong affiliative relationships to the number of times they gave aggression to other females. We conducted a GLMM analysis that assumed a negative binomial distribution, where the outcome variable was the number of times a male was aggressive to a female and the main predictor was their affiliation index. We accounted for time in association and cycling and non-cycling observation time by including these variables as additional main effects. The identities of males and females were included as random intercepts.

Effects of dominance rank and age on affiliative relationships

We investigated whether the strength and number of affiliative relationships males formed with unrelated females varied with male dominance rank and age. We began by examining whether young adult males were more likely than adolescent males to dominate females as assayed by pant grunting exchanges. To do so we conducted a generalized linear logistic regression analysis where the outcome variable was whether or not a male received a pant grunt from a particular female and the main predictor was the male's age. Male age was calculated as the midpoint of his age (in years) during the study. We controlled for the time pairs spent in association and observation hours by including these variables as an additional fixed effect in the model. Male and female identity were included as random intercepts. Next we determined whether the number of affiliative relationships males formed with females varied as a function of male age. Here we conducted a linear model analysis where the outcome variable was the total number of strong affiliative relationships a particular male had with females and predictors were the male's age and the number of hours the male was observed. Finally, we evaluated the effects male age and dominance relationships on the strength of male – female affiliative bonds by conducting a GLMM analysis where the outcome variable was the affiliation index of male - female pairs and the main predictors were the male's age and whether or not the female pant grunted to the male. We controlled for time in association and the time a female spent in estrus by including these variables as additional fixed effects. Male and female identity were added as random intercepts.

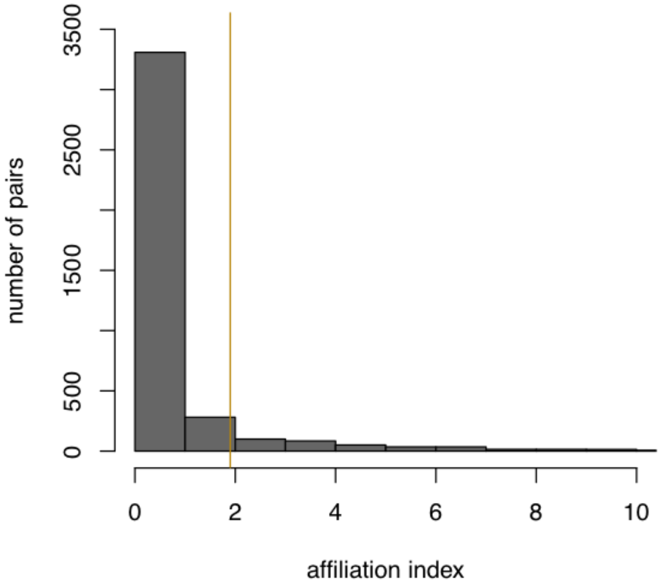
All analyses were conducted in R using the packages lme4 and lmerTest. To account for the varying scales of predictor variables in our multivariate analyses, we standardized all predictors by using their z-scores. In the following analyses, we report coefficient estimates and standard errors of predictor variables in summary tables. We also include p-values to aid interpretation of the results. We describe the impact of predictors on outcome variables as odds or incidence rate ratios.

Results

Affiliative relationships between adolescent and young adult males and females

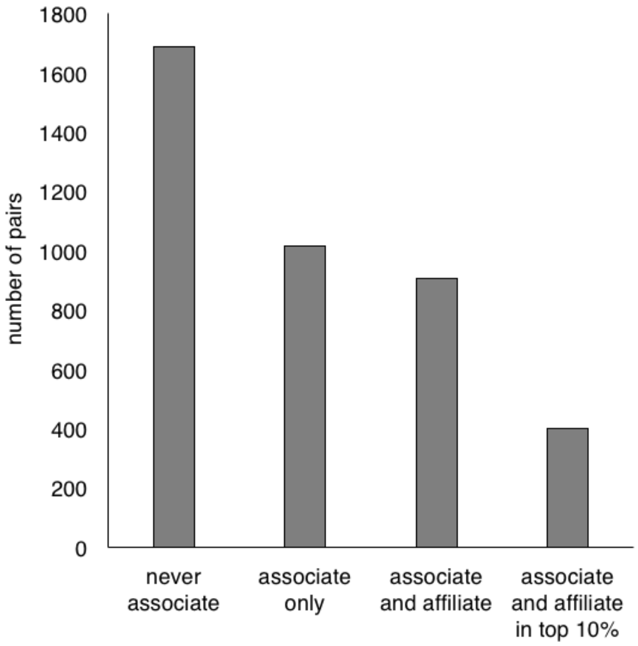
Figure 11a shows the distribution of affiliation indices between adolescent and young adult males and other mature individuals. Of these, 1,686 pairs never associated, 1,014 pairs associated but did not groom or maintain proximity, and 1,307 groomed and/or maintained spatial proximity (Figure 11b). All of the 30 adolescent and young adult males formed strong affiliative relationships with conspecifics as defined by pairs in the top 10% of the distribution of the affiliation indices (n = 401 of 4,007 pairs; Figure 12). Individual males formed strong bonds with 7 to 26 of the 136 mature individuals in the community (mean = 13.4 bonds per male, SD = 4.8). As documented in this and other chimpanzee communities, strong bonds existed between adolescent and young adult males and their mothers and maternal siblings (10% = 40/401) and between them and other mature males (54% = 217/401). Many strong affiliative relationships, however, existed between adolescent and young adult males and mature females who were not their mothers or their maternal sisters (36% = 144/401).

a)



number of pairs
0
500
1500
2500
3500
0
2
4
6
8
10
affiliation index

b)



number of pairs
1800
1600
1400
1200
1000
800
600
400
200
0
never associate
associate only
associate and affiliate
associate and affiliate in top 10%

Figure 11. a) Distribution of affiliation indices between adolescent and young adult male chimpanzees and all other mature individuals. Pairs that fall in the top 10% of all affiliation indices are to the right of the yellow line. Several pairs (68) with affiliation indices > 10 (range: 10.2 -135.1) are excluded from this figure to improve its clarity. b) Distribution of different types of pairs formed between adolescent and young adult male chimpanzees and all other mature individuals, including those with: 1) affiliation indices of zero who never associated; 2) affiliation indices of zero who did associate; 3) non-zero affiliation indices that fell within the bottom 90% of the distribution; and 4) affiliation indices that fell within the top 10% of the distribution.

The preceding obscures the fact that mature males, mature females, and maternal kin were not equally represented in the community. For example, there were 57 males and 78 females with whom focal males could form relationships. Males also had relatively few mature maternal kin living with them during this study, ranging from 0 – 4 chimpanzees per subject. We divided the number of times males formed affiliative relationships with different types of individuals by the total number of the latter to control for unequal availability. These calculations revealed that males frequently formed strong affiliative relationships with maternal kin when they had the opportunity to do so (mean = 77% of the time, SD = 33.6, n = 28 males). Adolescent and young adult males developed strong affiliative relationships with unrelated males (mean = 13% of the time, SD = 5.1, n = 30 males) and unrelated females less often (mean = 6% of the time, SD = 4.1, n = 30 males).

Virtually all of the adolescent and young adult males formed strong affiliative relationships with unrelated females. Twenty-eight of the 30 focal males formed a strong affiliative relationship with at least one mature female who was not his mother or maternal sister, and most males formed such relationships with multiple females (mean = 4.8 females, SD = 3.2, range: 0 – 12, Figure 12). In addition, 75% (23/30) of our male subjects, including all of the young adults, had at least one unrelated female among his top five partners (mean = 1.6 unrelated females in top 5, SD = 1.1, range = 0 – 4) as assessed by the affiliation index. Only two males failed to form a strong affiliative bond with an unrelated female. One of these males, Peewee (Figure 9), was an 11-year-old orphan; the other male, Cannonball, 9, was a young adolescent male whose mother associated infrequently with other chimpanzees (Figure 9). As noted above, females appeared 144 times with unrelated males in strong affiliative relationships. These 144 male-female pairs included 52 of the 78 mature females in the community, ranging from 11 to 57 years old (mean = 21.2 years, SD = 9.6). Fifteen of the 52 females were nulliparous and 37 had given birth.

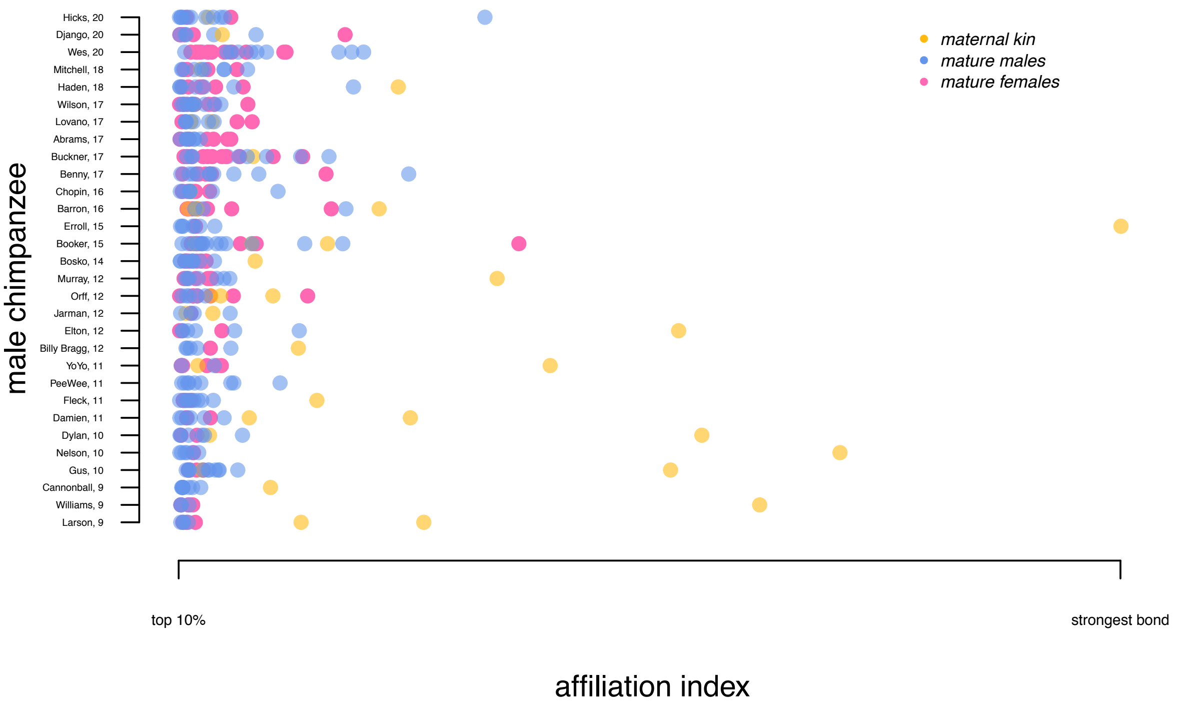


Figure 12. Chimpanzee pairs who fell in the top 10% of the distribution of affiliation indices. Indices are shown for 30 adolescent and young adult male subjects and different types of chimpanzees with whom they formed affiliative relationships, including maternal kin and mature males and females (n = 401 pairs).

Effects of female reproductive state on male – female bonds

The majority of females with whom males formed strong affiliative bonds had a full sexual swelling on at least one day during the study (90% of females = 47/52). They exhibited swellings when they were able conceive but also other times when they were pregnant and nursing an infant under 2 years old. Females in 85% (n = 123/144 pairs) of the strongly bonded pairs cycled during the study. Females in 45 pairs did so throughout the entire study (n = 15 females, including 10 nulliparas), while females in 78 pairs cycled for only portions of it (n = 29 females). Females in 21 pairs were anestrous throughout the study (n = 13 females).

Males maintained proximity to and groomed with females to whom they were strongly bonded irrespective of their cycling state. However, males maintained proximity slightly more often to females if they were cycling (n = 144 unique pairs, 78 including females in cycling and non-cycling states). Specifically, males maintained proximity to females when they were cycling at a mean rate of 0.33 scans per hour (SD = 1.1, n = 123 pairs). Males maintained proximity to their strongly bonded female partners when those females were not cycling as well (98/99 pairs = 99%), but at a mean rate of 0.13 scans per hour (SD = 0.13). A GLMM analysis that accounted for the amount of time females were in a given cycling state and male and female identity indicated that males maintained proximity to strongly bonded females 1.5 times more often, as assayed by scans, when females were cycling (Table 9a). In contrast, males groomed with females with whom they formed strong bonds at similar rates regardless of female reproductive state. Males groomed with females when they were cycling in 59% (73/129) of strongly bonded pairs at a mean rate of 0.48 minutes per hour (SD = 1.06). Alternatively, males groomed with females when they were not cycling in 63%

(62/99) of strongly bonded pairs at a mean rate of 0.23 minutes per hour (SD = 0.38). A GLMM analysis indicated that there was no effect of cycling state on how often males groomed with females (Table 9b).

Table 9. Factors affecting proximity and grooming. Results of GLMM analyses where outcome variables are: a) the number of times individuals in a pair were in close proximity and b) the number of minutes individuals in pairs spent grooming. Coefficients of predictor variables, their standard errors, and p-values are shown. Models included male and female identity as random intercepts and assumed a negative binomial distribution (n = 144 unique male-female pairs including 28 males and 52 females. Of these pairs, 78 appear twice, once when the female in pair was reproductively cycling and once where she was not).

a) Proximity

	Estimate	Std. Error	p-value
intercept	1.31	0.08	
female is cycling	0.39	0.13	0.003
observation time	1.35	0.14	<<0.001

b) Grooming

	Estimate	Std. Error	p-value
intercept	1.90	0.14	
female is cycling	0.26	0.25	0.30
observation time	0.72	0.34	0.01

Reassurance and vigilance

Males and females who formed strong affiliative relationships also engaged in friendly behaviors, such as reassurance. Individuals in 24% of the pairs (35/144) reassured each other, doing so 64 times (mean = 0.44 times / pair, SD = 1.1). Only 43 or 2% of the other 2,131 male-female pairs displayed reassurance behavior (mean = 0.02 times / pair, SD = 0.18). Results of a GLMM analysis revealed that for each unit increase in the affiliation index, reassurance between males and females increased by a factor of 2.1 after controlling for the amount of time males and females were in association and observation time (Table 10a).

Males and females who formed strong affiliative bonds also kept track of each other while traveling together by remaining vigilant. Individuals in 33% of these pairs (47/144) displayed vigilance while traveling 107 times (mean = 0.74 times / pair, SD = 1.65). Individuals in the remaining pairs did so only 99 times (mean = 0.05 times / pair, SD = 0.32) and involved far fewer dyads (3% = 70/2131). After controlling for the amount of time males and females were in association and observation time, a unit increase in the affiliation index resulted in vigilance between males and females increasing by a factor of 2.2 (Table 10b).

Table 10. Reassurance and vigilance. Results of GLMM analyses where outcome variables are: a) the number of times individuals in a pair reassured each other and b) the number of times individuals in a pair displayed vigilance while traveling. Coefficients of predictor variables, their standard errors, and p-values are shown. Models included male and female identity as random intercepts and assumed a negative binomial distribution (n = 2276 male-female pairs, including 30 males and 78 females).

a) Reassurance

	Estimate	Std. Error	p-value
intercept	-4.61	0.32	
pair's affiliation index	0.73	0.14	<<0.001
cycling observation time	0.06	0.18	0.721
non-cycling observation time	0.08	0.42	0.853

association	1.80	0.24	<<0.001

b) Vigilance

	Estimate	Std. Error	p-value
intercept	-3.97	0.25	
pair’s affiliation index	0.79	0.16	<<0.001
cycling observation time	0.19	0.16	0.231
non-cycling observation time	0.45	0.40	0.260
association	2.1	0.22	<<0.001

Grooming equability

By definition, most of the males and females who formed strong affiliative relationships groomed each other (79% of the pairs = 114/144). They did so for 0.29 minutes per hour on average (SD = 0.40, range = 0 to 3.3 min/hr). Males and females who did not share strong affiliative relationships also groomed, but only rarely (6% of pairs = 119/2131) and briefly (mean = 0.002 min/hr, SD = 0.01, range = 0 to 0.20 min/hr). In general, male-female grooming relationships were skewed as assessed by the grooming equality index (mean = 0.18, SD = 0.29, n = 233 pairs who groomed). Affiliative relationships, however, influenced the equability of grooming. Males and females who formed strong affiliative relationships groomed more equitably (mean = 0.27, SD = 0.32, n = 114 pairs) than did individuals who did not share a similar relationship (mean = 0.09, SD = 0.22, n = 119 pairs). Analyses indicated that the affiliation index predicted how equitably pairs groomed each other (Table 11). For each unit increase in the affiliation index, a pair's grooming equality index increased by a factor of 2.3 (Table 11).

Table 11. Grooming equality. Results of a GLMM analysis where the outcome variable is the grooming equality index. Coefficients of predictor variables, their standard errors, and p-values are shown. The model included male and female identity as random intercepts and assumed a negative binomial distribution (n = 233 pairs who groomed, including 30 males and 64 females).

	Estimate	Std. Error	p-value
intercept	-1.94	0.18	
pair's affiliation index	0.84	0.25	<<0.001
cycling observation time	1.10	0.46	0.016
non-cycling observation time	1.33	0.57	0.020
association	0.42	0.27	0.10

Male aggression toward females

While males reassured, kept track of, and groomed relatively more equitably with females with whom they affiliated, they behaved aggressively to them as well. Males directed aggression to females 103 times (mean = 0.72 times per pair, SD = 1.19, n = 144 pairs) in 40% of all strongly bonded pairs (57/144). These figures were higher than those displayed between males and females who did not share a strong affiliative relationship. In these cases, males displayed aggression to females 330 times (mean = 0.15 times per pair, SD = 0.77, n = 2131 pairs) in 7% of the pairs (154/2131). A GLMM analysis indicated that male aggression to females increased by a factor of 1.5 for every unit increase in their affiliation index when time in association and observation time were controlled (Table 12).

In addition to behaving aggressively to females with whom they shared strong affiliative relationships, adolescent and young adult males were more likely to fight over them compared to other females. Young males avoid challenging other males directly (e.g. Kawanaka, 1993; Sandel et al. 2017), and they did so only six times during focal observations. All cases involved one adolescent male attacking another when he mated or attempted to mate with a female with whom the other shared an affiliative relationship. Similarly, male subjects engaged in contact aggression with their maternal brothers very rarely, doing so only when one brother witnessed the other mating with a female who shared an affiliative relationship with both. These included one case where a late adolescent male subject attacked his younger adolescent brother and another where an adult male attacked his younger adult brother.

Table 12. Male aggression toward females. Results of a GLMM analysis where the outcome variable is the number of times a male directed aggression to a particular female. Coefficients of main predictors, their standard errors, and p-values are shown. The model included male and female identity as random intercepts and assumed a negative binomial distribution (n = 2276 male-female pairs including 30 males and 78 females).

	Estimate	Std. Error	p-value
intercept	-3.22	0.25	
pair's affiliation index	0.41	0.17	0.014
cycling observation time	0.28	0.14	0.051
non-cycling observation time	0.59	0.35	0.088
association	2.33	0.20	<<0.001

Effect of male age and dominance rank on affiliative relationships

Affiliative relationships between males and unrelated females changed as males aged. As they grew older, males became increasingly dominant to females. Females pant grunted to males in 12% (89/770) of all male-female pairs involving young adult males but in only 3% (51/1506) of male-female pairs involving adolescent males. For every unit increase in male age, a male became 2.8 times more likely to receive a pant grunt from an unrelated female (Table 13). Male subjects never pant grunted to a female.

Table 13. Dominance rank and male age. Results of a generalized linear logistic regression analysis where the outcome variable whether or not a male received a pant grunt from a particular female. Coefficients of main predictors, their standard errors, and p-values are shown. The model included male and female identity as random intercepts and assumed a binomial distribution (n = 2276 male-female pairs including 30 males and 78 females).

	Estimate	Std. Error	p-value
intercept	-4.35	0.29	
male age	2.81	0.41	<<0.001
association	2.52	0.24	0.26

observation time	0.21	0.38	<<0.001

The number of affiliative relationships males formed with unrelated females also increased with male age. Young adult males formed strong affiliative bonds with an average of 6.6 females (SD = 3.3, n = 10 males), while adolescent males formed similar bonds with 3.9 females (SD = 2.8, n = 20 males). Results of a linear model analysis revealed that a unit increase in male age resulted in male chimpanzees forming affiliative relationships with 3.03 more females (Table 14a). An additional analysis that controlled for male age indicated that the dominance rank relationships between males and females influenced the strength of their social bonds. The affiliation indices of pairs involving females who pant grunted to males were 1.8 times higher than those between pairs including females who never pant grunted to males (Table 14b). Nevertheless, male dominance was not required for bonds to exist. Females did not pant grunt to males in the majority of the strongly bonded male – female pairs, including 52 (34/66) and 77% (60/78) involving young adult and adolescent males, respectively.

Table 14. Variation in the number and strength of affiliative relationships. a) Number of affiliative relationships. Results of a linear model analysis where the outcome

variable is the number of affiliative relationships males formed with unrelated mature females. Effect sizes of predictor variables, their standard errors, and p-values are displayed (n = 30 males). b) Strength of affiliative relationships. Results of a GLMM analysis where the outcome variable is a pair's affiliation index. Coefficients of predictor variables, their standard errors, and p-values are displayed. This model included male and female identity as random intercepts and assumed a negative binomial distribution (n = 2276 male-female pairs, 30 males, 78 females).

a) Number of affiliative relationships

	Estimate	Std. Error	p-value
intercept	4.80	0.52	
male age	3.03	1.08	0.009
observation time	-0.56	1.08	0.612

b) Strength of affiliative relationships

	Estimate	Std. Error	p-value
intercept	-2.10	0.17	
male age	0.37	0.21	0.08
time female in estrus	0.44	0.25	0.08

association	2.50	0.13	<<0.001
male received pant grunt from female	0.59	0.08	<<0.001

Discussion

As described in other chimpanzee populations (Goodall, 1986; Hayaki, 1988; Pusey, 1990; Kawanaka, 1993; Nishida, 2011), adolescent and young adult male chimpanzees at Ngogo formed strong affiliative bonds with their maternal kin and other mature males (cf. Sandel et al., 2020). In contrast to males in other East African chimpanzee communities (e.g. Machanda et al. 2013), nearly all males at Ngogo also developed affiliative relationships with mature females who were not their maternal kin. These male-female pairs composed about one-third of all strong bonds formed by adolescent and young adult males and included most females in the community, who varied in age, parity, and reproductive state. Males maintained proximity to and groomed with their female partners not only when they were cycling, but also when they were pregnant and nursing young infants.

By definition, males and unrelated females who shared strong affiliative bonds often groomed each other and maintained close spatial proximity. They also touched each other in affectionate and reassuring ways, embracing when frightened and placing their hands on each other's backs while resting (cf. van Lawick-Goodall, 1968). They appeared intent on staying together and displayed vigilance while traveling, following and waiting for each other and looking back to one another frequently. Grooming between males and unrelated females was unbalanced in general, as is common for chimpanzees and especially for adolescent males (Watts, 2000; Sandel et al., 2020), but strongly bonded pairs groomed relatively more equitably compared to other pairs who groomed, a measure associated with long-lasting relationships between adult male chimpanzees (Mitani, 2009) and between female baboons (Silk et al., 2010). Importantly, males and females who shared strong bonds behaved in the preceding ways more often than males and females who did not share strong bonds, even when controlling for the time they spent together and the amount of time females spent cycling. In addition, affiliative behaviors that occurred infrequently between young males and unrelated females, such as food-sharing (n = 6 pairs) and agonistic support (n = 4 pairs), occurred primarily between individuals who had strong affiliative relationships (67% of food-sharing episodes; 75% of agonistic support). These preliminary observations regarding food-sharing and support are consistent with descriptions of relationships between male and female baboons and macaques who form friendships (Smuts, 1985; Haunhorst et al., 2016, Figure 13).

Figure 13. Bosko (right), an adolescent male chimpanzee, rests with Khutulun (left), a female with whom he shares an affiliative relationship. Photo by Jeremy Clift

While males affiliated with specific females, they also targeted them for aggression. Males behaved aggressively toward females with whom they shared strong affiliative relationships more often than they displayed aggression toward females with whom they did not share such relationships, even after accounting for the time individuals spent in association and female reproductive state. Female chimpanzees rarely received visible injuries from males during these incidents. Rather than inflict physical injury, these episodes appeared to ensure that females would fear males. Such intimidation is an important component of sexual coercion (Smuts and Smuts, 1993; Muller et al., 2007, 2011; Feldblum et al., 2014). By maintaining fear in these relationships, a male chimpanzee might be successful in taking a female on a sexual consortship (e.g. Tutin, 1979; Goodall, 1986) or preventing her from mating with other males (Smuts and Smuts, 1993; Muller et al. 2007, 2011; Feldblum et al., 2014).

The tendency of male chimpanzees to target their female social partners for aggression mirrors behavior in our own species. Men target their wives and female partners for physical abuse instead of other individuals with whom they spend comparable amounts of time in the same household (Wilson & Daly, 2009). Consequently, most violence women receive is from their intimate male partners, and this violence is considered a form of sexual coercion (Wilson & Daly, 2009; DeVries et al., 2013). Establishing whether male chimpanzee aggression toward their female social partners acts in a similar way and functions as sexual coercion will require further study. Importantly, we do not yet know how the aggressive or affiliative aspects of male-female chimpanzee relationships contribute to mating and reproduction. It is likely that the effects of aggression will change with male age, as older females often ignore aggression from young, adolescent males, who are still subordinate to them (Goodall, 1986; Pusey, 1990; Nishida, 2003, 2011; this study).

If adolescent males rely on affiliation to mate, they might invest in developing affiliative bonds with females more than young adult males. In contrast to this expectation, young adult males had strong affiliative relationships with a greater number of females than did adolescent males. Moreover, the strength of male – female bonds increased as males crossed the threshold into adulthood and became increasingly dominant to females. Taken together, these observations suggest that an asymmetry in rank may have facilitated the ability of males to form affiliative ties with females. Male dominance was not required for males to forge strong bonds with females, however, because adolescent males who did not yet clearly outrank females were able to do so, and females in the majority of strongly bonded pairs failed to pant grunt to their male partners.

It is possible that affiliative relationships between male and female chimpanzees, which begin in adolescence and young adulthood, last into prime adulthood. This, in turn, might explain why certain males and females at Ngogo who associate often have produced multiple offspring together, sometimes more than 10 years apart (Langergraber et al., 2013). Additional work will be needed to determine whether and how affiliative relationships contribute to male reproduction. Why young males at Ngogo form strong affiliative relationships with females also requires further investigation, as this finding does not accord with studies of other East African chimpanzee communities (e.g. Machanda et al., 2013). One possibility is that young males at Ngogo may have the opportunity to do so because female chimpanzees at Ngogo are more gregarious than females elsewhere, and the large size of the community gives them many more potential partners than in smaller communities (Langergraber et al. 2009; Langergraber et al. 2013). A second possibility is that we have focused on the behavior of adolescent and young adult males, who have not explicitly been the targets of study before regarding male-female social relationships in chimpanzees. A final possibility is that we may have observed a large number of affiliative bonds between males and females because many females cycled during this study, and males were simply attracted to females for mating purposes. The unusually large number of cycling females we observed was due to two factors. A disease outbreak led to seven females losing their infants (Negrey et al., 2019), causing them to resume cycling. In addition, Ngogo is an extremely productive habitat, and food is often readily available for chimpanzees there (Watts et al., 2012; Wood et al., 2017; Potts et al., in press). During periodic food bonanzas created by high levels of fruit availability, female chimpanzees frequently resume cycling even when they have small infants and are unlikely to conceive (Ngogo Chimpanzee Project, unpublished data). Although our analyses suggest that female reproductive state alone cannot explain the existence of the affiliative relationships between males and unrelated females, these findings are preliminary as they are based on limited observations of interactions between males and non-cycling females. Determining whether male-female bonds persist when females are unable to conceive will require additional research and remains an important topic for future study.

In sum, results of this study indicate that adolescent and young adult male chimpanzees form affiliative bonds with unrelated females. These bonds are similar to, yet different, from those formed between adult males and maternal kin because males direct aggression selectively toward their female partners. These findings add to a body of literature on male-female social bonds in primates, which are known to improve male mating success and offspring survival (Smuts, 1985; Palombit et al., 1997; Palombit, 2009; Nguyen et al., 2009; Huchard et al., 2010; Ostner et al., 2013). Our results also shed new light on the evolution of social bonds between human females and males, which can involve both affiliation and coercive violence (Smuts, 1995, Wilson & Daly 2009, DeVries 2013).

Chapter 5

The Development of Affiliative and Coercive Reproductive Tactics in Male Chimpanzees

Note on Publication

Chapter 5 has been submitted for publication as a co-authored research article. My co-authors are my dissertation committee member, Dr. Kevin Langergraber (K. L.), Dr. Aaron Sandel (A.S.), assistant professor of anthropology at the University of Texas at Austin, Dr. Linga Vigilant (L.V.), research scientist at the Max Planck Institute for Evolutionary Anthropology, and my dissertation chair, Dr. John Mitani (J.M.). K.L. contributed to the development of the study, conducted the paternity analyses, and helped write the manuscript. A.S. contributed to the development of the study and helped write the manuscript. L.V. supervised the genetic analyses. J.M. planned the study, collected behavioral data, and helped write the manuscript.

Abstract

Like many animals, adult male chimpanzees compete for a limited number of mates and often achieve this through force. They fight other males as they strive for status that confers reproductive benefits and use aggression to coerce females to mate with them. Nevertheless, small-bodied, socially immature adolescent male chimpanzees, who cannot compete with older males for status nor intimidate females, father offspring. We investigated how they do so through a study of adolescent and young adult males at Ngogo in Kibale National Park, Uganda. Adolescent males mated and reproduced primarily with nulliparous females, who are not preferred as mating partners by older males. In addition, two other factors, affiliation and aggression, influenced mating success. Specifically, the strength of affiliative bonds that males formed with females and the amount of aggression males directed toward females predicted male mating success. The effect of male aggression toward females on mating success increased as males aged, especially when they directed it toward females with whom they shared affiliative bonds. These results mirror sexual coercion in humans, which occurs most often between males and females involved in close, affiliative relationships.

Introduction

Throughout the animal kingdom, males use their strength, size, and status to compete for mates (Darwin 1871; Trivers 1972; Clutton-Brock 1988). Winners in direct combat are typically the largest, strongest, most-experienced males (e.g. African elephants (*Loxodonta africana*): Hollister-Smith et al. 2007; migratory terns (*Sterna hirundo*): Becker et al. 2008; fallow deer (*Dama dama*): Komers et al. 1997). Because of their superior size and strength, males can also injure females and coerce them to mate (e.g. elephant seals (*Mirounga angustirostris*): LeBoeuf & Mesnick 1991; multiple species of waterfowl: McKinney et al. 1983; bighorn sheep (*Ovis canadensis*): Hogg 1984, dolphins (*Tursiops* spp): Mann et al. 1996; orangutans (*Pongo pygmaeus*): Mitani 1985; reviewed in: Smuts & Smuts 1993; Clutton-Brock & Parker 1995; Palombit 2014). Young, small males, however, are unable to coerce females sexually and instead adopt alternative mating tactics (Gross 1996). For example, small male marine iguanas (*Amblyrhynchus cristatus*) masturbate before mating to achieve speedy ejaculation (Wikelski & Baurle 1996). Mid-sized crustacean males (*Paracerceis sculpta*) take on the appearance of females and mate with them while living in disguise within a larger male's "harem" (Shuster & Wade 1991). For animals that develop slowly, reproductive tactics may shift during development. For example, young male bushbucks (*Tragelaphus scriptus*) sneak copulations with females, but later grow up to defend groups of females and territories (Apio et al. 2007).

Our closest living relatives, chimpanzees (*Pan troglodytes*), develop very slowly. They live in relatively stable groups or communities, whose members form temporary subgroups that change in size and composition (Nishida 1968; Goodall 1986). Because single females mate with multiple males, sperm competition ensues (Tutin 1979; Harcourt et al. 1981; Hasegawa & Hiraiwa-Hasegawa 1983). In addition, adult males employ two behavioral tactics that increase their chances of mating and reproducing. First, they compete with others for status, and high dominance rank yields mating opportunities (Bygott 1974; Tutin 1979; Goodall 1986; Muller 2002). Second, adult males use aggression to intimidate females and coerce them to mate with them, sometimes leading females away from other males on extended consortships (Tutin 1979; Goodall 1986; Smuts & Smuts 1993; Muller et al. 2007, 2011; Feldblum et al. 2014; Kaburu et al. 2015, but see Stumpf & Boesch 2010). Consequently, high-ranking males sire more offspring than low-ranking males (Constable et al. 2001; Boesch et al. 2006; Wroblewski et al. 2009; Newton-Fisher et al. 2010; Langergraber et al. 2013), and males are more likely to father offspring with females to whom they direct aggression (Feldblum et al. 2014).

Adolescent male chimpanzees between 8 and 15 years old are still physically and socially immature and therefore cannot compete effectively with larger, stronger adult males. Their small size and reduced strength may also prevent adolescent males from sexually coercing females. By age 16, males have typically finished growing and can dominate females, but as young adults (16-20 y), they still occupy low ranks in the male dominance hierarchy (Goodall 1986; Kawanaka 1993; Watts 2018). Despite these disadvantages, adolescent and young adult male chimpanzees sire a nontrivial number of offspring (Constable et al. 2001; Boesch et al. 2006; Wroblewski et al. 2009; Newton-Fisher et al. 2010; Langergraber et al. 2012, 2013; Muller et al. 2020). How they do so is not fully clear.

One tactic young males adopt is to selectively pursue specific females as mating partners. In this context, nulliparous, adolescent female chimpanzees cycle for many years without conceiving and often lose their first offspring (Pusey 1997; Emery Thompson 2013; Wood et al. 2017; Walker et al. 2018). Adult males typically show little sexual interest in these females (Muller et al. 2006; 2020). Adolescent male chimpanzees consequently target nulliparous females as mating partners and primarily reproduce with them (Watts 2015; Muller et al. 2020). Nevertheless, this strategy cannot explain adolescent and young adult male mating and reproductive success completely because young males also father the offspring of parous females (Wroblewski et al. 2009; Langergraber et al. 2013; Muller et al. 2020).

A second, non-mutually exclusive possibility is that young male chimpanzees mate by forming affiliative bonds with females. Males living at Ngogo in Kibale National Park, Uganda, forge affiliative bonds with females during adolescence and young adulthood (Reddy & Mitani 2020). Males in both age groups also target their female partners for aggression (Reddy & Mitani 2020). It is currently unclear whether the affiliative or aggressive aspects of these relationships contribute to the mating success of young male chimpanzees. Prior research suggests this as a possibility as adult male and female chimpanzees who frequently associate and range in the same areas of the Ngogo communal territory often produce offspring together (Langergraber et al. 2013).

The Ngogo chimpanzee community is extremely large, including many adolescent and young adult males. This creates an ideal opportunity to investigate the reproductive strategies employed by young male chimpanzees. In this paper, we start by examining adolescent and young adult male chimpanzee mating behavior and reproduction to determine whether they favour nulliparous over parous females. Specifically, we investigate whether adolescent males father the offspring of first-time mothers and whether this changes as males grow older and higher ranking. We then proceed to examine how affiliation and coercive aggression influence male mating success from adolescence through adulthood.

Methods

Study Site

Research took place at Ngogo in Kibale National Park, Uganda, a mid-altitude rainforest (Struhsaker 1997). Members of the Ngogo chimpanzee community occupy a territory of approximately 35 km^2 (Mitani et al. 2010). Male chimpanzees have been followed continuously since 1995, and females identified and regularly followed since 2004. The community size has ranged between 140 - 219 chimpanzees (Wood et al. 2017, Ngogo Chimpanzee Project, unpublished data). The ages of natal individuals younger than 20 years old are known within one day to one year, while the ages of older individuals are estimated based on their genetic relationships to other individuals, physical appearance, and behavior (Wood et al. 2017). Immigrant females are estimated to be 13 years old when they enter the community (Wood et al. 2017).

Behavioral Observations

Behavioral data on the affiliative and aggressive social interactions between male chimpanzees and females and their influence on mating success were derived from focal observations made by R.R. over 17 months during June-August 2015 and June 2016-August 2017. Twenty adolescent (9-15 years old) and 10 young adult male chimpanzees (16-20 years old) were focal subjects. Males were considered adolescent if their testes were visible and enlarged (Pusey 1990). Each male was followed for at least 25 hours (mean ± SD = 47.6 ± 6.6 hours per focal; range: 25-61 hours) and on at least 19 different days (mean ± SD = 33.8 ± 6.2 days per focal; range: 19-47 days). During focal observation sessions, R.R. recorded behavioral interactions between adolescent and young adult males and other community members, including 78 mature females who were not their mothers or maternal sisters (n = 2,276 total dyads). Females were considered mature if they had begun to exhibit sexual swellings, which was around 11 years old. Sixty-two of these mature females were parous or gave birth for the first time during the study, while 16 were nulliparas.

During focal following sessions, we recorded all chimpanzees who were observed together with the focal male during the hour-long focal following episodes. These individuals were defined to be in association, or in the same subgroup, with focal subjects (cf. Chapman et al. 1994; Mitani et al. 2002; Sandel et al. 2020). Chimpanzees within 5 meters to focal subjects were recorded every 10 minutes during instantaneous point samples, and the amount of time focal subjects gave and received grooming was noted to the nearest second. We recorded all observed instances of aggression directed by focal males to mature females. We quantified male aggression as the number of times males threatened, displayed, charged, chased, hit, kicked, and bit females (van Lawick-Goodall 1968; Muller et al. 2007). We also recorded mating and noted daily whether females in association with focal subjects had full sexual swellings.

To quantify the strength of affiliative bonds between focal males and other adolescents and adults in the community (N = 136 individuals, N = 4,007 dyads), we used the frequency with which pairs groomed and maintained spatial proximity to create a composite affiliation index, adapted from Silk and colleagues (2006a):

$$\frac{\left(\frac{\mathrm{G}ab}{\mu\mathrm{G}} + \frac{\mathrm{P}ab}{\mu\mathrm{P}}\right)}{2}$$

The numerator of the first term indicates the rate (minutes per focal observations) male *a* groomed and received grooming from individual *b*; its denominator indicates the mean grooming rate for all dyads in the community. The numerator of the second term indicates the rate (proportion of instantaneous point samples) male *a* was in proximity to individual *b* and its denominator indicates the mean proximity rate for all dyads in the community.

Analyses

Male dominance rank

Data on rank relationships between adult males come from focal observations made by J.M. between 2003-2018 on 62 adult males. He assigned yearly ordinal ranks to males if they had reached adulthood (i.e. 16 y old) and were observed making pant grunts, calls given by subordinate individuals to higher-ranking individuals (Bygott 1974). To account for the number of males in the hierarchy each year, we standardized males' yearly ordinal ranks by subtracting the male's ordinal rank (r) from the total number of adult males present in the community that year (n_M), and dividing this number by one less than the total number of males in the community that year (Muller et al. 2006):

$$(n_{M}-r)/(n_{M}-1).$$

During years where a conception occurred but a male's rank was missing due to incomplete observations but his subsequent year's rank was available, we averaged the previous and subsequent year's standardized ranks. When a subsequent year's rank was unavailable (e.g. the male had died) we used the previous years' standardized rank. We replaced missing ranks for 5 males in the preceding manner in 9 instances, representing 0.001% of 4744 total siring opportunities.

Paternity success

We assigned paternity to 105 offspring born since 2003 after all possible sires were genotyped. We conducted likelihood-based parentage analyses (Kalinoswki et al. 2007) using 19-44 autosomal microsatellites typed from faecal samples collected non-invasively from chimpanzees. Paternities were determined in earlier research (N = 91: Langergraber et al. 2007, 2009, 2013, 2017) or newly generated for this study (N = 14) following previously published methods. Most offspring (77% = 81/105) had a parous mother at the time of their conception. Twenty-four had mothers known or assumed to be nulliparous based on behavioral observations, the female's estimated age, and the median age at first birth reported for East African chimpanzees who emigrate (16 years; Walker et al. 2018).

We determined how often adolescent and adult males of varying ages and ranks sired offspring with nulliparous and parous females. To do so, we conducted two mixed effects logistic regression analyses where the outcome variable was whether a male was the father of an infant he had the opportunity to sire. We considered males who were at least 9 years old at the time of the infant's conception as potential fathers because this is the age of the youngest known sire in chimpanzees (Langergraber et al. 2012; Muller et al. 2020). We also excluded males as potential sires of infants born to their mothers, as this type of close inbreeding has not been documented at Ngogo and occurs rarely in chimpanzees elsewhere (Walker et al. 2017). We were interested in both age and rank as indicators of a male's ability to win in direct male-male competition, but male rank and age were correlated (Spearman's rho = 0.77, $p \ll 0.001$). We therefore conducted two analyses, one that included only age at the time an infant was conceived as a predictor, and one that included only rank as a predictor. For the purposes of the latter analysis, we set the ranks of adolescent males and young adults who had not entered the hierarchy to zero because adolescent males almost never receive pant grunts from adult males and rarely engage in dominance interactions between themselves (Hayaki 1988; Sandel et al. 2017).

Factors affecting male mating success

We employed a model comparison approach to investigate the effects of female parity and male-female social relationships on male mating success. We included only females who exhibited full estrous swellings and were able to mate (N = 57 females, 14 nulliparas, 43 primaparas and multiparas, 1,671 pairs), and assayed male mating success by the number of times males and females mated.

We used seven variables, including male age, female parity, the number of times a male directed aggression toward a female, the pair's affiliation index, the time these individuals spent together in association, and the time a female spent in estrus, to create 19 candidate models (Supplemental Table 2), all of which assumed a negative binomial distribution. Male age was defined as his median age (in years) across the study period and was included in most of the models (17/19), as the effect of male age on mating success is a central focus of this analysis. Females were assigned to two parity categories, nulliparous or parous, and female parity appeared in half of the models (47% = 9/19) to assess its hypothesized influence on male mating activity. To evaluate the roles of affiliation and aggression on mating success, we included a pair's affiliation index and the number of times the male was aggressive to the female as fixed effects in one third (32% = 6/19) of the candidate models. We included only one of these variables in eight of the models and neither in five others. We also included association as a fixed effect in half of the models (47% = 9/19) to control for the possibility that large effects of affiliation and aggression on mating success might simply reflect frequent association between specific pairs. Association by itself is an important measure of chimpanzee sociality and predicts reproduction between males and females (Langergraber et al. 2013). Including it as an additional fixed effect in seven models and excluding it in three others where aggression, the affiliation index, or both appeared permitted us to evaluate its impact. We also constructed two models that included association but excluded the affiliation index, male aggression, and both as fixed effects to assess whether association alone rather than male aggression toward females and affiliation explained male mating success. In all of the candidate models except one, we controlled for the number of days a female had a sexual swelling by including this as a fixed effect.

In addition to the preceding seven variables, we considered four interactions between them in 17 of the candidate models. Because male chimpanzees mate less often with nulliparous females as they grow older and enter adulthood (e.g. Muller et al. 2006; Watts 2015), we included an interaction between male age and whether or not a female was nulliparous as fixed effects in nine candidate models. To determine whether the effects of affiliation and aggression on mating success changed with male age, we included an interaction between each of the three social relationship variables (aggression, affiliation, and association) and male age in all models where social variables appeared (9-10 models). Finally, because aggression might work differently for females with whom males have strong compared to weak affiliative bonds (Reddy & Mitani 2020), we included an interaction between the affiliation index and the number of times the male was aggressive to the female in three of the models. For all 19 models, we controlled for observation effort by including this as an offset and for male and female identity by including them as random intercepts.

We used Akaike's information criterion, corrected for small sample size (AICc), to determine the best approximating model(s). We report coefficient estimates and standard errors and plot incidence rate ratios for all predictor variables in the model with the lowest AICc value to estimate their effects.

All analyses were conducted in R using the packages lme4, and MuMIn (Barton 2009; Bates et al. 2015; R Core Team 2017). To account for the varying scales of predictor variables in our multivariate analyses, we centred and standardized all predictors by using their z-scores, subtracting each data point from the mean and dividing this value by 2 times the standard deviation (Gelman & Hill 2007).

Results

Effects of age and rank on paternity

Adolescent male chimpanzees fathered 9% (9/105) of the infants in our sample, a considerably smaller proportion than would be expected by chance (32% =

1531/4744 of siring opportunities that were available to adolescent males). Adolescent males primarily fathered the infants of nulliparous mothers (6/9 = 67%), who conceived about a quarter of all offspring in our sample (23% = 24/105). This changed as males transitioned to adulthood and grew increasingly high-ranking, as adult males sired proportionately fewer offspring with nulliparous females than they did with parous females. Only 29% (10/34) of the offspring fathered by young adult males between 16 and 20 years old had nulliparous mothers, while older adult males (> 20 years) produced even fewer of their offspring with first-time mothers (13% = 8/62). These proportions were considerably lower for high-ranking adult males defined as those in the upper third of the dominance hierarchy with standardized ranks greater than or equal to 0.67 (cf. Muller et al., 2006). All of these high-ranking males were older than 20 years old and rarely fathered offspring of first-time mothers (6% = 2/35 offspring; Figure 1).

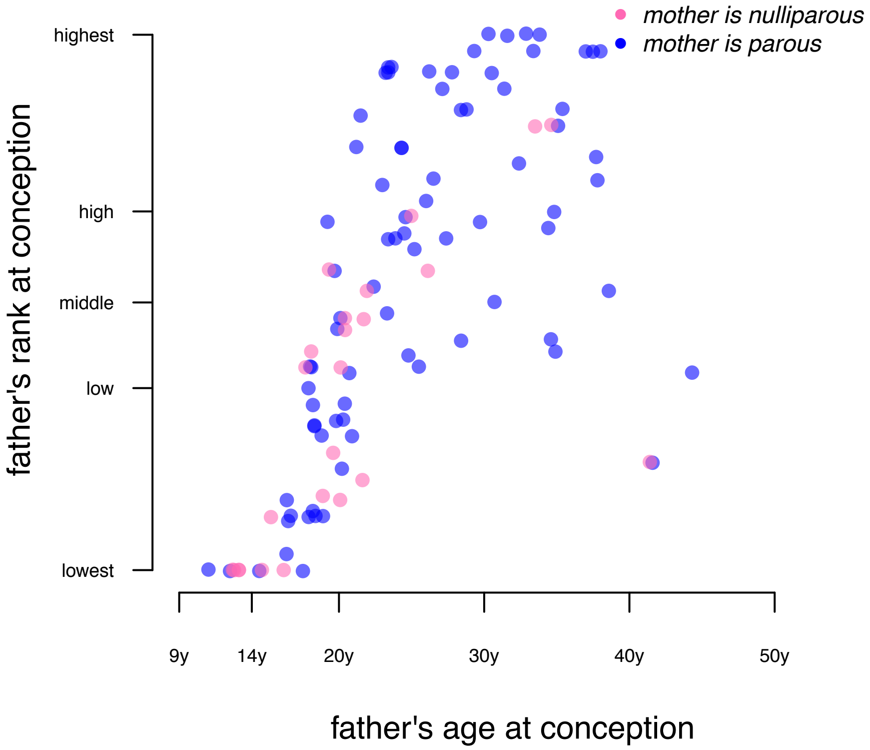


Figure 14. Father’s rank and age at time of conception for offspring born to nulliparous mothers (pink) and multiparous mothers (blue) (N = 105 offspring). Adolescent males (<16 y) who have not entered the male hierarchy are those in the “lowest” rank category, while low-ranking males are those with a standardized rank <0.34, high-ranking males are those with standardized ranks >0.67 and middle-ranking males are those in-between (Muller et al. 2006

Two analyses indicated that both age and rank influenced the probability that males fathered infants of nulliparous females. A mixed effects logistic regression analysis that accounted for the number of opportunities males had to sire offspring indicated that a one-year increase in a male's age decreased his probability of fathering an infant born to a first-time mother by a factor of 1.03 (Figures 14 and 15). An additional analysis indicated that an increase in a male's rank decreased the probability that he fathered an infant born to a first-time mother by a factor of 1.28 (Figures 14 and 15).

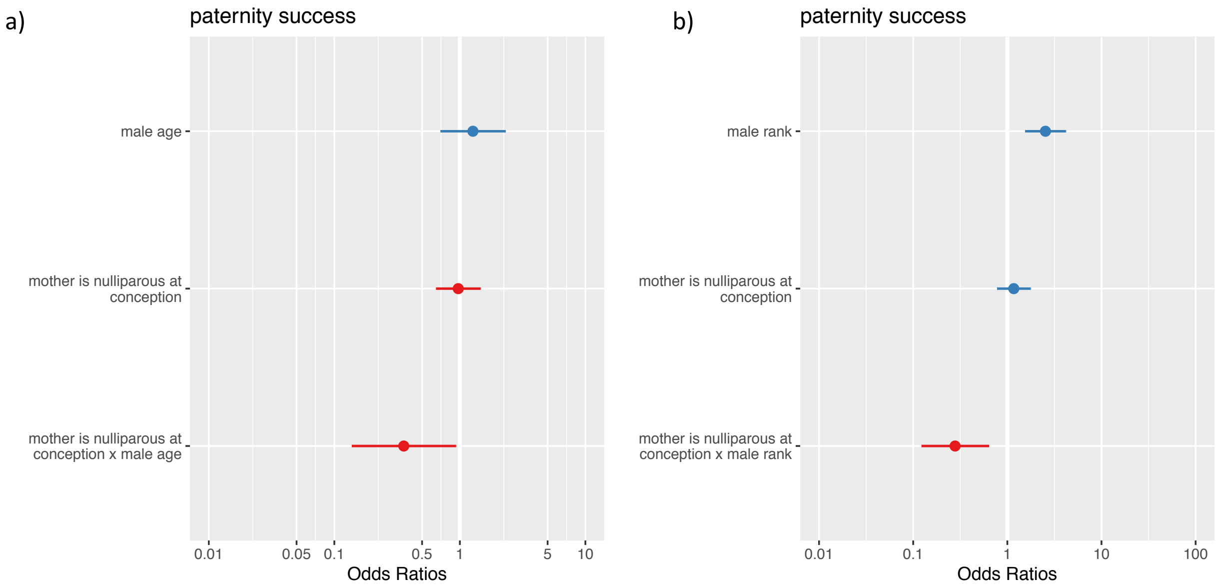


Figure 15. Odds ratio plots showing main effect predictors for mixed effects logistic regression models where the outcome variable was whether a male sired a particular infant he had the opportunity to sire and predictors included a) male age or b) male

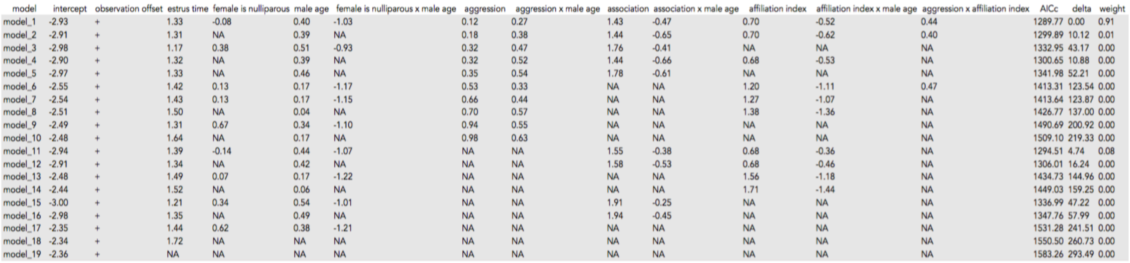
rank. (N = 4,744 fathering opportunities, 76 males, 58 mothers, 105 offspring, 24 born to first-time mothers)

Effects of female parity, male aggression, and affiliation on mating success

Mating occurred 339 times in 12% (197/1671) of potential pairs formed between 20 adolescent and 10 young adult males and 57 reproductively active females (mean = 0.20 times per pair, SD = 0.74). Pairs that mated had higher affiliation index scores (mean = 2.54, SD = 4.83) than pairs that did not mate (mean = 0.42, SD = 1.71). In addition, males behaved aggressively more often to females with whom they mated than to other females. On average, male aggression occurred 0.73 (SD = 1.23) times per pair in which mating occurred and 0.15 (SD = 0.73) in pairs that never mated. Younger males mated more frequently with nulliparous females than did older males. Mating occurred on average 0.50 times (SD = 1.3) in adolescent male-nulliparous female pairs compared to 0.17 times (SD = 0.65) in young adult male-nulliparous female pairs.

A model comparison analysis indicated that the best approximating model with the lowest AICc value included all 7 variables and 4 interactions (Table 14, Figure 16). Its Akaike model weight (91%) was considerably higher than that of any of the other 18 models (Table 14). Only one other candidate model that excluded male aggression toward females and the interaction between aggression and other variables displayed some explanatory power, with a relatively small Akaike model weight of 8% and Δ AICc from the best approximating model of 4.7 (Table 14).

Table 15. Results of a model selection analysis where outcome variable was the number of times a specific pair of male and female chimpanzees mated. Models are ranked by their AICc values.



model	intercept	observation offset	estrus time	female is nulliparous	male age	female is nulliparous x male age	aggression	aggression x male age	association	association x male age	affiliation index	affiliation index x male age	aggression x affiliation index	AICc	delta	weight
model_1	-2.93	+	1.33	-0.08	0.40	-1.03	0.12	0.27	1.43	-0.47	0.70	-0.52	0.44	1289.77	0.00	0.91
model_2	-2.91	+	1.31	NA	0.39	NA	0.18	0.38	1.44	-0.65	0.70	-0.62	0.40	1299.89	10.12	0.01
model_3	-2.98	+	1.17	0.38	0.51	-0.93	0.32	0.47	1.76	-0.41	NA	NA	NA	1332.95	43.17	0.00
model_4	-2.90	+	1.32	NA	0.39	NA	0.32	0.52	1.44	-0.66	0.68	-0.53	NA	1300.65	10.88	0.00
model_5	-2.97	+	1.33	NA	0.46	NA	0.35	0.54	1.78	-0.61	NA	NA	NA	1341.98	52.21	0.00
model_6	-2.55	+	1.42	0.13	0.17	-1.17	0.53	0.33	NA	NA	1.20	-1.11	0.47	1413.31	123.54	0.00
model_7	-2.54	+	1.43	0.13	0.17	-1.15	0.66	0.44	NA	NA	1.27	-1.07	NA	1413.64	123.87	0.00
model_8	-2.51	+	1.50	NA	0.04	NA	0.70	0.57	NA	NA	1.38	-1.36	NA	1426.77	137.00	0.00
model_9	-2.49	+	1.31	0.67	0.34	-1.10	0.94	0.55	NA	NA	NA	NA	NA	1490.69	200.92	0.00
model_10	-2.48	+	1.64	NA	0.17	NA	0.98	0.63	NA	NA	NA	NA	NA	1509.10	219.33	0.00
model_11	-2.94	+	1.39	-0.14	0.44	-1.07	NA	NA	1.55	-0.38	0.68	-0.36	NA	1294.51	4.74	0.08
model_12	-2.91	+	1.34	NA	0.42	NA	NA	NA	1.58	-0.53	0.68	-0.46	NA	1306.01	16.24	0.00
model_13	-2.48	+	1.49	0.07	0.17	-1.22	NA	NA	NA	NA	1.56	-1.18	NA	1434.73	144.96	0.00
model_14	-2.44	+	1.52	NA	0.06	NA	NA	NA	NA	NA	1.71	-1.44	NA	1449.03	159.25	0.00
model_15	-3.00	+	1.21	0.34	0.54	-1.01	NA	NA	1.91	-0.25	NA	NA	NA	1336.99	47.22	0.00
model_16	-2.98	+	1.35	NA	0.49	NA	NA	NA	1.94	-0.45	NA	NA	NA	1347.76	57.99	0.00
model_17	-2.35	+	1.44	0.62	0.38	-1.21	NA	NA	NA	NA	NA	NA	NA	1531.28	241.51	0.00
model_18	-2.34	+	1.72	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1550.50	260.73	0.00
model_19	-2.36	+	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1583.26	293.49	0.00

Further examination of the variables in the best approximating model suggests that affiliative bond strength was positively associated with the number of times male chimpanzees mated and that its effect on mating success changed with male age (Supplemental Table 3, Figure 3). Specifically, a unit increase in a male's affiliation index with a particular female increased the frequency with which he mated with her by a factor of 2. Alternatively, the impact of the affiliation index on mating success decreased by a factor of 0.60 with each unit increase in male age.

Compared to affiliation, aggression had a positive but weak impact on mating success (Figure 16). Nevertheless, male aggression toward females became more effective as males grew older. For each unit increase in male age, the impact of aggression on mating success increased by a factor of 1.31 (Figure 3, Figure 4). Finally, aggression that males directed toward females with whom they shared strong affiliative bonds had a larger influence on males' mating success than aggression males directed toward other females. For every unit increase in a pair's affiliation index, aggression by males toward females increased their frequency of mating by a factor of 1.54 (Figures 16 and 17).

Consistent with results of the long-term paternity analysis, the best approximating model also revealed that males mated less often with nulliparous females as they entered adulthood. For each unit increase in male age, males decreased the frequency with which they mated nulliparous females by a factor of 0.35 (Figures 16 and 17).

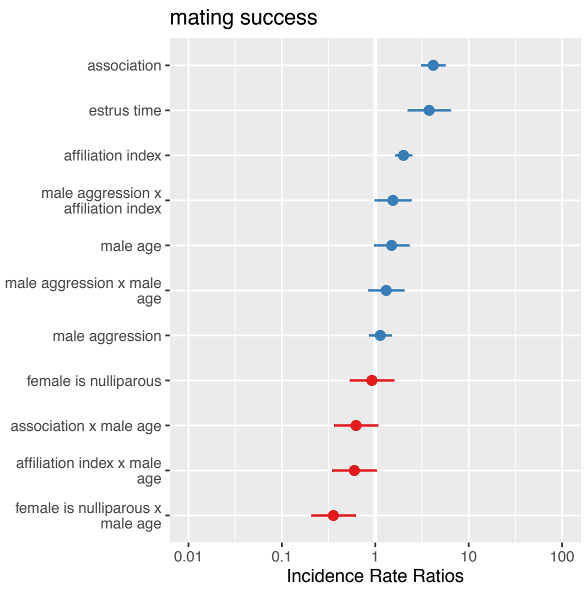


Figure 16. Incidence rate ratio plot showing main effect predictors for the generalized linear mixed model that had the lowest AICc value and comprised 91% of the model weight in a comparison of 19 models (Table 14), where the outcome variable was the number of times males and females mated (n = 1,671 male-female pairs including 20 adolescent males, 10 young adult males, 57 reproductively available females, 14 of whom were nulliparas)

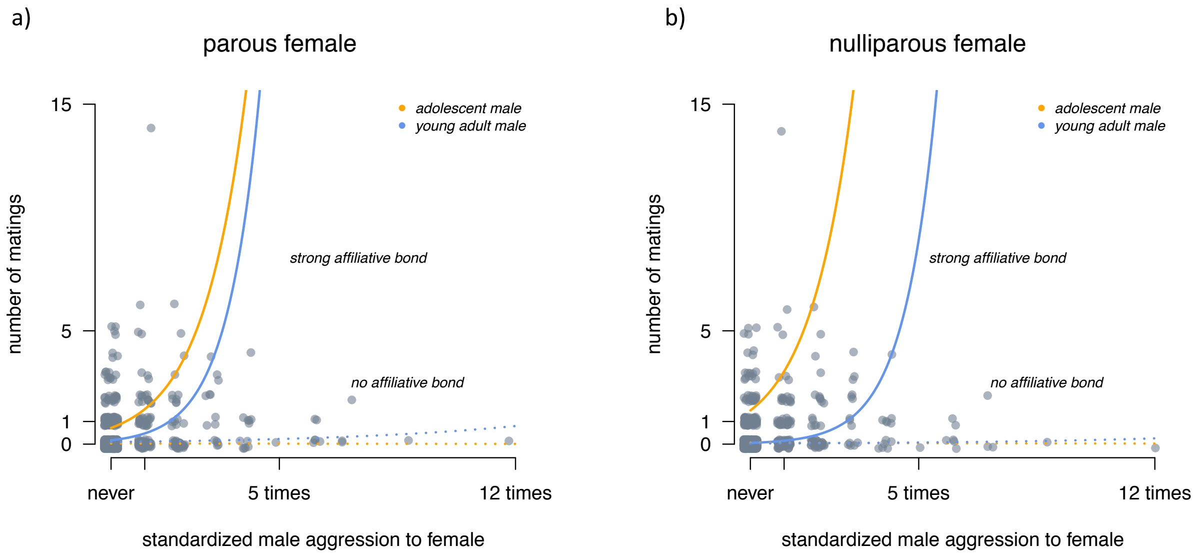


Figure 17. Mating frequency of adolescent and young adult males and a) parous females and b) nulliparous females by the number of times the male in a pair directed aggression to the female. Lines illustrate predictions of mating frequency based on GLMM coefficients (Table 14, Figure 16) for an adolescent (set to 9 yrs) and a young adult (set to 20 yrs) with a female with whom he does or does not have a strong affiliative bond. Affiliation index is set to 0 for "no affiliative bond" lines and to one standard deviation above the mean affiliation index for the "strong affiliative bond" line. Association values, estrus time, and observation time are set to the mean

values from the dataset for all prediction lines. Affiliation and age were both continuous variables in all analyses but are displayed categorically here for illustrative purposes

Discussion

The results presented here suggest that adolescent male chimpanzees, who cannot effectively compete with older males nor sexually coerce adult females, employ two behavioral tactics to mate and reproduce. First, as reported in previous research, adolescent males appear to target adolescent, nulliparous females as mating partners; they mate with nulliparous females frequently and father their offspring more often in adolescence than they do in adulthood (Watts 2015; Muller et al. 2020). Our findings also corroborate past research indicating that nulliparous female chimpanzees are less preferred as mating partners than are parous females. Specifically, as male chimpanzees transition from adolescence to adulthood and rise in dominance rank, they show less sexual interest in nulliparous females and target them for aggression infrequently (Muller et al. 2006). High-ranking males also rarely father their offspring (Constable et al. 2001; Boesch et al. 2006; Wroblewski et al. 2009; Newton-Fisher et al. 2010; Langergraber et al. 2013; Muller et al. 2020; this study). Second, mating success for adolescent and young adult males was predicted by the strength of affiliative bonds that males formed with females. Male aggression, in contrast, had a relatively weak relationship to mating success, but one that grew stronger as males grew older and increasingly dominant to females. The relationship between aggression and mating success also grew stronger as the affiliative bond between the male and the female to whom he directed aggression increased.

These findings increase our understanding of the nature of sexual coercion in chimpanzees. We have recently shown that adolescent and young adult males selectively direct aggression toward females with whom they form strong affiliative bonds (Reddy & Mitani 2020). Here, we demonstrate that aggression has little effect on mating success outside of these bonds and for younger males who are not yet physically mature and unlikely to dominate females (Pusey 1990; Nishida 2003; Reddy & Mitani 2020). Instead, mating success increases when a young adult male directs aggression to a female with whom he shares a bond and can dominate.

These results complement prior research that indicates aggression, mating, and reproduction are linked in chimpanzees (Muller et al. 2007; Feldblum et al. 2014; Kaburu et al. 2015) and clarify the role that affiliation plays in creating those linkages. Specifically, sexual coercion is more effective when adolescent and young adult males have affiliative bonds with the females they attack. One reason may be that females suffer costs if they refuse to mate with their male bond partners (Smuts & Smuts 1993). The nature of these costs remains to be explored. Nor is it clear whether and how affiliative relationships with males benefit female chimpanzees. It is important to note that our findings are consistent with patterns of intersexual aggression in other species where males are highly aggressive to females with whom they share bonds. This includes hamadryas baboons (*Papio hamadryas*), where females live in one-male groups, and most social activity is directed by the single males in these groups, i.e. "leader males." After being attacked by their leader male, hamadryas females appear fearful and follow him even more closely than they had previously (Swedell & Schreier 2009). In our own species too, many women are subject to frequent sexual coercion by their male partners, but often remain in such relationships for reasons that vary widely (Wilson & Daly 2009).

Scant data exist about the proximate psychological mechanisms that underlie male aggression and female compliance in chimpanzees. However, investigating these proximate mechanisms may provide information about how bonds that affect paternity in chimpanzees might lead to a human-like social system (Smuts 1995). Our preliminary observations are consistent with the hypothesis that male aggression toward their social partners is psychologically motivated by sexual possessiveness (e.g. Wilson & Daly 2009), and that females have a psychologically distinct experience when attacked by a male with whom they have an affiliative bond. For example, adolescent and young adult males make direct attacks on male peers infrequently, but when they do so, it is when another male mates or attempts to mate with one of their female social partners

(Reddy & Mitani 2020). Anecdotally, when female chimpanzees received aggression from an adult male who did not have a strong affiliative bond with them, they often just screamed and ran away. Females receiving similar aggression from a male with whom she shared a strong affiliative relationship, however, react in an entirely different way. When attacked, these females remain in place, lunge toward their male partners while clutching their arms, rocking back and forth, and screaming repeatedly until making choking sounds.

An important limitation of this study is that we cannot evaluate the relative impacts of affiliation and aggression on adolescent male paternity success. Only seven males in this study have reproduced thus far, siring 15 offspring, creating a small sample to make strong inferences. Our preliminary findings based on this small sample suggest that males who affiliate with and direct aggression to specific females gain a reproductive advantage with those females, but additional data are clearly needed. As these data accumulate, evaluating the effects of affiliation and aggression on male reproduction will be complicated because additional factors that we have not considered will require examination. For instance, we are likely to have underestimated the importance of sexual coercion, as it may act to ensure mating exclusivity as well as increasing a male's ability to mate with a specific female (Smuts & Smuts 1993). In this context, aggression is often used to initiate consortships in chimpanzees, where males lead females away from other community members and mate with them exclusively for several days (e.g. Tutin 1979). The challenge of maintaining exclusivity is not uniform. It may be relatively easy for high-ranking males because fewer males will challenge them to mate, or easier to do with nulliparas, who are not preferred mating partners (Muller et al. 2006). Additional study of the causes and consequences of sexual coercion will add to our ability to assess the relative impacts aggression and affiliation have on male chimpanzee reproductive success.

Our findings also provide insights into the evolution of human pair bonds. Although the mechanisms that ensure paternity certainty in our species are diverse, including intimate partner violence (Smuts 1995, Wilson & Daly 2009, DeVries et al. 2013) and larger cultural structures (e.g. religion: Bamshad et al. 1998, Strassman et al. 2012), our finding that affiliative bonds between males and females appear entwined with sexual coercion in one of our two closest living relatives suggests that this aspect of intersexual relationships may be embedded deeply in our past.

Chapter 6.

Conclusion & Future Directions

This dissertation investigated the social development of adolescent and young adult male chimpanzees, with an emphasis on how social relationships males form with females influence their ability to mate and reproduce. This research includes one of the largest datasets collected on adolescent male chimpanzee social behavior in the wild. My findings provide insights into how mother-son bonds develop and change in a male-dominated primate species, the caregiving capacities of male chimpanzees, and how affiliative bonds between males and females and sexual coercion are entwined and affect male mating and reproduction.

In Chapter 2, I documented how mother-son relationships changed during adolescence and later as males crossed the threshold to adulthood. Specifically, I showed that adolescent males gradually break their bonds with their mothers, relying on them less and less for agonistic and emotional support during conflicts. Although adult male chimpanzees continue to affiliate with their mothers occassionally, they forged their strongest relationships with individuals other than their mothers, including unrelated females and other males (Chapter 4).

The functional significance of the social bonds formed between mothers and their adolescent and adult sons is unclear. One possiblity is that mothers continue to play a role in their sons lives, impacting them in fitness-enhancing ways during adolescence. Recent studies have shown that maternal presence improves the growth and survival of their sons through adolescence (Samuni et al. 2020; Stanton et al. 2020). Adolescent males may also gain reproductive advantages from maternal support. For example mothers may help their sons form social bonds with unrelated females. Sons might affiliate with females who share close social relationships with their mothers, and subsequently mate and sire offspring with these females (Chapters 4 and 5). Additionally, the agonistic support adolescent sons receive from their mothers may help them achieve dominance over females. Determining whether and how mothers contribute to their adolescent sons' fitness requires further investigation.

In the second chapter of this thesis, I described what happens when maternal-offspring bonds are broken due to maternal death. Specifically, I examined how maternal loss altered social relationships between adolescent and young adult males and their vulnerable, juvenile siblings. Most adolescent and young adult male subjects who had younger siblings played with and groomed them while their mothers were alive. For four males, these typical sibling relationships underwent a major shift when their mothers died during a respiratory outbreak. Following the outbreak, males groomed and reassured their younger siblings at higher rates that they had previously. Males also constantly looked out for their orphaned siblings' safety and became distressed when separated from them. In sum, adolescent and young adult males took on a parental-like role in the lives of their younger siblings.

The preceding findings provide insight into the evolution of paternal care in humans. In our species, males provide considerable care to immature individuals, who are often their own offspring. Offspring care is not a prominent facet of male chimpanzee behavior. However, the proclivity of adolescent and young adult males to provide maternal-like care to their younger, orphaned siblings suggests that male chimpanzees possess the motivations and ability to engage in such behavior in certain situations. In an early hominin ancestor, male caregiving behavior may have been displayed in similar fashion to vulnerable maternal kin as well as other individuals that males recognized as their kin, including their own offspring. Offspring recognition could be faciliated by males forming bonds with the mothers of their offspring, like those I describe in chapters 4 and 5 of this dissertation (see also Chapais 2011; Langergraber et al. 2013). Additional research is necessary to determine whether male chimpanzees form differentiated relationships with the immature offspring of their female social partners and whether they provide fitness benefits to males, immatures, or both.

In the final two chapters of this thesis, I describe heretofore undocumented affiliative social relationships between adolescent and young adult male chimpanzees and unrelated females and the impact these relationships have on male mating and reproduction. I found that young male chimpanzees mated with the same females with whom they formed affiliative, and occasionally aggressive, relationships. Virtually all of my 30 subjects had at least one female with whom he affiliated in multiple ways, even when controlling for the time they spent together and the female's reproductive state. Affiliation between males and females included maintaining close spatial proximity, grooming frequently and equitably, reassurance, and keeping track of each other during travel. Males also showed aggression to the same females with whom they affiliated, shaking branches to intimidate them, charging and chasing them, and occasionally hitting, kicking, and biting them.

As shown in Chapter 5, affiliative and aggressive behavior directed toward specific females predicted male mating success. Males frequently mated their close female social partners and those to whom they directed aggression. However, affiliation and aggression were associated with mating success differently as males grew older and increasingly dominant to females. Affiliative behavior had the largest effect on the mating success of young adolescent males. The relationship between aggression and mating success strengthened with male age and when males outranked females, but aggression had the strongest influence on mating success when it occurred between pairs who shared a strong affiliative bond.

These findings lead to several unresolved questions. First, do the affiliative relationships between adolescent and young adult male chimpanzees and females persist over time? Second, do male-female pairs who form these relationships produce multiple offspring over many years, as has been previously documented at Ngogo (Langergraber et al. 2013)? Third, what benefits, if any, do females derive from these relationships? One possibility is that females receive protection from males when their infants are vulnerable to infanticide. Within-group infanticide is a significant source of infant mortality in chimpanzees, and females with newborn infants sometimes associate with specific males, including their adult sons and the fathers of their offspring (Murray et al. 2016; Wellens 2017; Wood et al. 2017). My own observations indicate that some females seek the company of males with whom they have affiliative relationships within one week after giving birth. For example, when these new mothers joined a party of chimpanzees, they displayed fearful and anxous behavior such as panting, grimacing, whimpering, and screaming. They avoided most adult males and females, moving away from them if approached. For males with whom they formed strong bonds, however, these same mothers displayed the opposite behavior. They approached these males and sought frequent physical contact and reassurance, such as embraces. Males also initiated reassurance by putting their arm around the female and groomed females for extended periods, often peering at the newborn infants. While traveling, females maintained unusually close proximity to these males. One female walked alongside a male while pressing her shoulder against his. She moved with him so consistently that she followed him on a boundary patrol into a neighboring territory. Another female built and slept in a night nest next to her male partner on consecutive nights after giving birth. These anecdotal observations include only a few individuals. More observations are needed to determine whether females, who have recently given birth, seek the company and support from their male partners and whether bonds formed between females and males contribute to infant survival.

A final question concerns whether male chimpanzees form relationships with the offspring of their female social partners. If so, does this represent a proto-form of paternal care? One recent study suggests that fathers may affiliate with their adolescent sons (Sandel et al. 2020). When males start to become independent from their mothers and start to follow adult males, they preferentially groom their fathers (Sandel et al. 2020). This behavior is potentially faciliated by male-female relationships and associations described in chapters 4 and 5 and by Langergraber and colleagues (2013). My preliminary observations suggest that males affiliate with the dependent offspring of their female social partners. These males groomed, provided reassurance, and played with the offspring of their female partners more frequently than with other similarly-aged infants and juveniles. On a few occassions, males also shared food, carried, and defended these same immatures against aggression. Future studies are necessary to determine whether fathers interact nonrandomly with their offspring and if such interaction provides benefits to immatures.

Results of this research increase our understanding of male chimpanzee reproductive strategies and social development during adolescence. My findings also have important implications for understanding male-female social relationships in our own species. During adolescence, male chimpanzees grow independent from their mothers and form bonds with unrelated females. Males and females who affiliate mate and produce offspring together. Males also groom, comfort, and play with the offspring of females to whom they are bonded; these same offspring are likely to have been fathered by these males. Male chimpanzees also dominate females and occasionally use coercion to control their sexual behavior. For humans, too, bonds between males and females can involve affiliation, co-parenting, and sometimes coercive violence.

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