

**Male-Male Relationships and the Transition to Adulthood
in Chimpanzees**

by

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DEDICATION

To my mom and dad.

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ABSTRACT

Strong social bonds play an important role in primate behavior. These bonds feature prominently in the lives of adult male chimpanzees (*Pan troglodytes*). Male chimpanzee friends form coalitions, share food, join each other on territorial border patrols, and help each other as they attempt to rise in the dominance hierarchy. Despite the importance of friendship and dominance rank in adulthood, scant information exists regarding how they develop. Do social bonds with other males form early in life? Do males start to jockey for position in the dominance hierarchy before they reach adulthood? For one year, I observed male chimpanzees transitioning to adulthood at Ngogo in the Kibale National Park, Uganda. In contrast to adults, adolescent male chimpanzees do not compete for status with their peers. Instead, they prioritize affiliative relationships. Adolescent and young adult males form social bonds with maternal brothers, as do older adult males. Unlike middle-aged adult males, however, adolescent and young adult males forge some of their strongest bonds with old males rather than with their peers. Unexpectedly, some of the strongest grooming relationships were between adolescent and young adult males and their fathers. Because chimpanzees mate promiscuously, there is no reason to suspect that male chimpanzees can recognize their fathers or that fathers can recognize their sons. These unsuspected grooming bonds appear to emerge, in part, due to past relationships formed when adolescent and young adults were infants and juveniles. Adolescent and young adult males joined subgroups with older males who occupied similar parts of the

territory as their mothers in the past. They also groomed formerly high-ranking males. Thus, as males transition to adulthood they form bonds with old, formerly high-ranking males with whom they are familiar. These findings raise the intriguing possibility that fatherhood may have evolved from an ape-like social system.

CHAPTER 1

Introduction

Social bonds are an integral part of being human. We form long-term bonds with family and non-family members alike. The strong bonds formed between humans facilitate the development of language, culture, and other types of complex social behaviors (Bell and Coleman 1999; Hruschka 2010). Strong social bonds also play an important role in non-human primate behavior (Seyfarth and Cheney 2012). Social bonds or “friendships” describe any type of consistent, affiliative behavior between two individuals, and are determined through measures of association, spatial proximity, grooming, and other behaviors, such as cooperation (Seyfarth and Cheney 2012; Silk et al. 2013; Silk 2002). Previous research has provided important insights into the nature and significance of animal social bonds. In cercopithecine monkeys, strong social bonds occur primarily between maternal relatives (Chapais and Berman 2004; Gouzoules 1984; Silk 2007). Where kin are unavailable, individuals form bonds with non-kin, as in male macaques (*Macaca assamensis*, Schülke et al. 2010) and in female horses (*Equus caballus*, Cameron et al. 2009). These bonds have significant physiological and fitness consequences. Female chacma baboons (*Papio ursinus*), who form strong social bonds with others, display lower stress levels than do females who form weak bonds (Crockford et al. 2008; Wittig et al. 2008). In addition, female baboons (*P. cynocephalus*, *P. ursinus*), who forge strong social ties with conspecifics, live longer and give birth to infants who survive more than do females with weak bonds (Silk 2007; Silk et al. 2009; Silk et al. 2010; Silk et al. 2003).

Adult male chimpanzees (*Pan troglodytes*) also form strong social bonds with conspecifics (Goodall 1986; Mitani 2009; Nishida 1979). Adult male chimpanzee social bonds, like those in other primates, can be defined by time spent in close proximity and grooming. Kinship influences the formation of friendships, with maternal half-siblings frequently displaying strong social bonds. Nevertheless, male chimpanzees also forge these relationships with non-relatives (Langergraber et al. 2007). In fact, bonds between several pairs of male chimpanzees have been observed to persist over many years, and some of the most enduring social bonds occur between non-kin (Mitani 2009). Age and status are two factors that affect the formation of social bonds between unrelated males, with peers and individuals who are similar in dominance rank frequently forming these relationships (Mitani 2009; Mitani et al. 2002).

Male chimpanzee social bonds confer fitness benefits, as bonded partners cooperate in interactions within and between communities. Within communities, males cooperate via short-term coalitions and long-term alliances that influence the acquisition and maintenance of high dominance rank (Nishida 1983; Nishida and Hosaka 1996). High rank, in turn, is positively related to male reproduction (Boesch et al. 2006; Langergraber et al. 2013; Newton-Fisher et al. 2010; Wroblewski et al. 2009). Male chimpanzee friends also cooperate during territorial border patrols (Watts and Mitani 2001). Patrols result in lethal attacks on neighbors, which can lead to subsequent territorial expansion (Mitani et al. 2010). Such take-overs increase the amount of food available to females, which affects male reproductive success in the process (Williams et al. 2004).

Although a considerable amount of information is known about adult male chimpanzee social relationships, important questions remain concerning how these social relationships develop. Adult male chimpanzees constantly strive for status, as the dominance hierarchy permeates all

aspects of their lives (Bygott 1979; Nishida 1983; Riss and Goodall 1977). Few data, however, exist regarding how peer and kin support between adult male chimpanzees originates. Are its roots embedded deeply in ontogeny? Does support obtained in adolescence facilitate a male chimpanzee's ability to transition into the social world of adults? Because social bonds are a significant part of adult male chimpanzee life, when and how they emerge are two central, yet unanswered, questions. A critical phase to examine is the period of adolescence when male chimpanzees become independent from their mothers and begin their transition into the world of adult males.

This thesis addresses four questions: 1) Do adolescent male chimpanzees display decided dominance relationships with their peers? 2) Do male chimpanzees forge social bonds during adolescence or only as adults? 3) With whom do adolescent and young adult males form these bonds? 4) What factors influence the formation of social bonds during the transition to adulthood?

Defining adolescence

There is no universally agreed upon definition of adolescence in nonhuman primates. Some primatologists avoid the term altogether, referring to independent individuals who are between juvenility and adulthood as "subadults" (e.g., Alberts and Altmann 1995). Other researchers acknowledge adolescence as a discrete life history stage in primates, most often in apes (Bernstein et al. 1991; Pusey 1990; Setchell and Lee 2004; Watts and Pusey 2002). Here I recognize adolescents as individuals who are reproductively *capable* but who have not yet successfully reproduced (Pereira and Altmann 1985; Setchell and Lee 2004). Another defining feature is that adolescents are still growing. Pereira and Altmann (1985, p. 261) define

adolescents as “pubertal, pre-reproductive individuals.” Similarly, based on their study of variation in testosterone among male rhesus macaques (*Macaca mulatta*), Bernstein et al. (1991, p. 35) define adolescence “as a period during which subjects are still undergoing significant physical growth in stature, dentition, and muscle mass, along with a gradual maturation of their gonadal endocrine systems,” concluding that “these males may be fertile but should not be considered adult.” Building on these definitions in light of life history theory (Charnov 1991), I consider a biological definition of adolescence as the period between the onset of puberty and the attainment of full body size.

In male chimpanzees, early adolescence begins with the onset of puberty, which is apparent from increases in testes size around 8 years of age (Pusey 1990). Determining the end of adolescence and beginning of adulthood, however, is not straightforward. Male chimpanzees in the wild are considered adults around 16 years when they dominate adult females (Goodall 1986), reach full body size (Pusey 1990), and become integrated into the social world of adults (Muller and Wrangham 2004). Nevertheless, there is considerable variation associated with these events.

For the purposes of this study, I consider male chimpanzees between the ages of 8 and 16 years to be adolescents. Using categorical age cut-offs are not ideal for studying adolescence (Dorn et al. 2006), but many studies, including this one, are limited by the data available. Additional rationales for these age categories are provided in the respective chapters of this thesis. Given the range of ages covered in this study, subjects encompass the transition to adulthood, and provide a foundation for understanding the behavioral changes that occur during this period. Future work is required to investigate how these social changes relate to physical and physiological changes. The focus of this dissertation is on social relationships.

Study site and subjects

This dissertation is based on fieldwork that I conducted over the past five years at Ngogo in Kibale National Park, Uganda. The results presented here are largely from data that I collected from August 2014 through August 2015. Ngogo lies at the center of the Kibale and is covered mostly by old growth rainforest interspersed by regenerating forest and grasslands (Struhsaker 1997). The chimpanzee community at Ngogo is an ideal population for a cross-sectional study of adolescent male social behavior. Ngogo is larger than any other chimpanzee community described to date, nearly three times the size of most other groups (Patterson et al. 2014; Wilson et al. 2014). For most of the study period, it consisted of 193 individuals, including 31 adult males, 23 adolescent males, 63 adult females, 15 adolescent females, 10 juvenile males, 5 juvenile females, and 46 infants. I focused observations on ten middle and late adolescent male chimpanzees (mean \pm SD = 14.3 \pm 1.1 years, range = 12.4 to 15.7 years) and eight young adult male chimpanzees (mean \pm SD = 18.8 \pm 1.1, range = 17.3 to 20.7 years). I limited data collection to a subset of adolescent and young adult males to maximize the number of observation hours on each subject. A detailed description of the research methods is provided in the three chapters that address my central research questions.

The development of dominance and social bonds in chimpanzees

Prior studies of chimpanzees suggest that during adolescence, males avoid vying for status with age-mates (Bygott 1979; Hayaki et al. 1989). In contrast, a prior study at Ngogo found that adolescent male chimpanzees formed a hierarchy among peers (Sherrow 2012). One important limitation of that prior study was that the age of male subjects were unknown at the time and

estimated. Re-evaluation of the ages of these individuals now suggests that some of the subjects were actually young adults (Wood et al. 2017). In Chapter 2, I evaluate dominance relationships between adolescent male chimpanzees of known age at Ngogo. To do so, I used observations of aggressive behavior and a formal signal of submission, the pant grunt (Bygott 1979; De Waal 1982). I discovered that adolescent male chimpanzees do not form a hierarchy with their peers. I discuss possible explanations for why male chimpanzees exhibit relatively low levels of aggression with other adolescents and apparently delay forming decided dominance relationships with their peers until adulthood.

Although adolescent males fail to strive for status with peers, it remains unclear whether they form affiliative relationships. Chimpanzees are social at an early age. Infants spend time playing with their siblings and other infants when they are available (Goodall 1986). This is especially true for males (Lonsdorf et al. 2014). Juveniles subsequently interact with age-mates and other conspecifics during play (Hayaki 1985), but social interactions are largely controlled by the mother. Because of the fission-fusion nature of chimpanzee society, mothers dictate whether their infants will have any opportunities to be with others (Brent et al. 1997; Pusey 1983). Juveniles may succeed in “convincing” their mother to join parties with other juveniles or adult males (Goodall 1986; Lonsdorf et al. 2014), but infants and juveniles will have few chances to form bonds with conspecifics beyond their mother and her other dependent offspring.

During adolescence the social world of the young male changes drastically. Adolescent male chimpanzees are, for the first time, free to choose with whom to associate. Adolescence is a trying time for male chimpanzees, as they attempt to integrate themselves into the social worlds of adults. They spend less time with their mother and more time with adult males, although when they are with adult males they remain at the periphery of the group and are rarely groomed

(Kawanaka 1989; Pusey 1990; Sherrow 2008). Previous research has shown that some adolescents associate selectively with specific adult males rather than age-mates or individuals of similar rank, and in these cases, partners are not always kin (Hayaki 1988; Kawanaka 1993; Nishida 2012; Pusey 1990). These observations are illuminating, but general principles about who forms bonds with whom have not emerged, as only small numbers of adolescents have been subjects of study at any given time. For example, only 4-8 adolescents were observed at a time in previous studies (Kawanaka 1989; Pusey 1983; Pusey 1990), constraining the ability to investigate partner preference.

In adult male chimpanzees, age, rank, and kinship influence the formation of social bonds (Mitani 2009; Mitani et al. 2002). There are good reasons to suspect that adolescent male chimpanzees will form strong social bonds with maternal brothers and peers when given the opportunity. Because male chimpanzees are philopatric and adults form strong social bonds with age-mates (Mitani 2009; Mitani et al. 2002), males may forge these ties earlier during adolescence. As noted above, prior research has not been able to investigate when bonds form because only small numbers of adolescents have been observed. It is also unclear if the bonds adolescent males form with adults are comparable to the strong social bonds that adult males have with each other. From the limited evidence currently available, the adolescent-adult bonds differ from those formed between adults; adolescents appear to be followers rather than friends (Goodall 1986).

In Chapter 3, I demonstrate that adolescent male chimpanzees form social bonds with other adolescent and adult males. Social bonds are based on the subgroups that they join, as well as spatial proximity and grooming relationships. The bonds that middle and late adolescents forge with other males do not differ from those of young adult male chimpanzees. I show that

adolescent and young adult males form bonds with their maternal brothers, old males, some peers, and, surprisingly, their fathers. The grooming bonds with fathers appear to be initiated by sons, as they are responsible for grooming their fathers, and fathers rarely groom them. What explains adolescent and young adult male chimpanzees' relationships with old males, particularly fathers?

In Chapter 4, I provide evidence that adolescent and young adult male chimpanzees join subgroups with older males who had used a similar part of the territory as their mothers in the past when adolescent and young adults were infants and juveniles. In addition, past rank of the older male partly explains the paternal grooming bias. I discuss these behavioral mechanisms for paternal recognition, and consider the implications for the evolution of human kinship patterns.

In the Conclusion, I present a synthesis of the results, and the implications for kin recognition in chimpanzees and the evolution of human social bonds. I also discuss future directions of research that arise out of this work.

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CHAPTER 2¹

Adolescent male chimpanzees do not form a dominance hierarchy with their peers

ABSTRACT

Dominance hierarchies are a prominent feature of the lives of many primate species. These hierarchies have important fitness consequences, as high rank is often positively correlated with reproduction. Although adult male chimpanzees (*Pan troglodytes*) strive for status to gain fitness benefits, the development of dominance relationships is not well understood. While two prior studies found that adolescent males do not display dominance relationships with peers, additional research at Ngogo in Kibale National Park, Uganda, indicates that adolescents there form a linear dominance hierarchy. These conflicting findings could reflect different patterns of rank acquisition across sites. An alternate possibility arises from a recent re-evaluation of age estimates at Ngogo and suggests that the report describing decided dominance relationships between adolescent males may have been due to the accidental inclusion of young adult males in the sample. To investigate these issues, we conducted a study of 23 adolescent male chimpanzees of known age during 12 months at Ngogo. Adolescent male chimpanzees exchanged pant grunts, a formal signal of submission, only 21 times. Recipients of pant grunts were late adolescent males, ranging between 14 and 16 years old. In contrast, younger adolescent males never

¹ Sandel, A.A., Reddy, R.B., Mitani, J.C. (2017) Adolescent male chimpanzees do not form a dominance hierarchy with their peers, *Primates*, 58: 39-49.

received pant grunts from other males. Aggression between adolescent males was also rare. Analysis of pant grunts and aggressive interactions did not produce a linear dominance hierarchy among adolescent males. These data indicate that adolescent male chimpanzees do not form decided dominance relationships with their peers and are consistent with the hypothesis that the hierarchy described previously at Ngogo resulted from inaccurate age estimates of male chimpanzees. Because dominance relationships develop before adulthood in other primates, our finding that adolescent male chimpanzees do not do so is surprising. We offer possible explanations for why this is the case and suggest future studies that may help clarify the matter.

INTRODUCTION

Many social animals, including primates, form dominance hierarchies (Bernstein 1976). Some of the best information regarding dominance relationships derives from studies of Old World monkeys (Subfamily Cercopithecinae, Altmann 1962; Samuels et al. 1987). Here adult male and adult female cercopithecine monkeys establish separate dominance hierarchies (Hausfater et al. 1982; Koford 1963; Seyfarth 1976). For males, competition for rank can be especially intense (Gesquiere et al. 2011) because high rank confers fitness benefits. In several primate species, high-ranking males reproduce more than do low-ranking males (Alberts 2012).

Given the important fitness consequences of high rank for adult primates, considerable attention has been given to its development. Studies of cercopithecine monkeys, including baboons (*Papio* spp.) and macaques (*Macaca* spp.), reveal that dominance relationships form early during development in both females and males (Cheney 1977; Johnson 1987; Koyama 1967; Pereira 1988; Pereira 1989; Pereira 1995). Female baboons and macaques remain in their

natal communities for life. As juveniles, they acquire and maintain ranks adjacent to their kin with the help of their mothers and maternal relatives (Berman 1980; Chapais 1988; Cheney 1977; Datta 1988; Horrocks and Hunte 1983; Lee and Oliver 1979). Like their sisters, juvenile and adolescent male baboons and macaques also obtain support from their mothers before they disperse to new groups. However, in contrast to females, a male's size and age are often better predictors of his dominance rank than is his mothers' rank (Johnson 1987; Koford 1963; Pereira 1989). While still living in their natal groups as juveniles and adolescents, male baboons and macaques display aggression to peers, using competitive asymmetries due to size and age to dominate others (Johnson 1987; Lee and Oliver 1979; Pereira 1995).

Studies of adult male chimpanzees (*Pan troglodytes*) have shown that they too strive for status, forming dominance hierarchies in the process (Bygott 1979; Goodall 1986; Mitani 2009; Newton-Fisher 2004). As adults, male chimpanzees acquire their dominance rank using aggression and coalitionary behavior (Goodall 1986; Hayaki et al. 1989; Muller and Wrangham 2004a; Muller and Wrangham 2004b; Nishida 1983; Nishida and Hosaka 1996). Once established, male chimpanzee dominance relationships are commonly acknowledged by a call, the pant grunt. Pant grunts are formal signals of submission and are always directed up the hierarchy given unidirectionally by a subordinate chimpanzee to a dominant one (Bygott 1979; De Waal 1982; Noë et al. 1980). Adult male chimpanzees compete vigorously with each other because, as is the case with cercopithecine monkeys, high status confers reproductive benefits. High-ranking males typically produce more offspring than do low-ranking males (Boesch et al. 2006; Duffy et al. 2007; Langergraber et al. 2013; Newton-Fisher et al. 2010; Wroblewski et al. 2009). Despite the importance of dominance relationships for adult male chimpanzees, scant information exists about its development.

Male chimpanzees take a long time to grow up. As they do so, they remain in their natal groups. For the first eight to ten years of their lives, male chimpanzees travel almost constantly with their mothers (Pusey 1983; Pusey 1990), joining and leaving other community members throughout the day in the fission-fusion pattern characteristic of chimpanzees (Goodall 1983; Nishida 1968). As infants and juveniles, chimpanzees interact with other community members, but these interactions are largely influenced by the social relationships and status of their mothers (Lonsdorf et al. 2014; Murray et al. 2014). Infants begin to give pant grunts to adults during their first few months of life. While still being carried ventrally by their mothers, they will sometimes pant grunt in tandem with their mothers as they approach a high-ranking male (Nishida 2012). Juvenile and adolescent chimpanzees also give pant grunts to adult males when greeting them (Pusey 1990).

Male chimpanzees start to become socially independent during adolescence (Goodall 1986; Pusey 1983; Pusey 1990). Although mothers and sons can maintain life-long social bonds, they travel less often together when males reach adolescence. By age 12 or 13, adolescent males predominantly follow adult males throughout the territory or travel alone (Hayaki 1988; Kawanaka 1989; Pusey 1983; Pusey 1990). Between this time and adulthood, adolescent males' dominance relationships with adult community members change drastically. At the start of adolescence, male chimpanzees are small and are unable to dominate adult females. During this time, they are especially submissive to adult males. By the end of adolescence, males appear to have reached adult height (Sandel, unpublished data) but continue to increase in body weight (Pusey et al. 2005). At this point, they are able to dominate all community females and start to challenge adult males for a position in the adult male hierarchy (Goodall 1986; Muller and Wrangham 2004a). Although these details regarding the social relationships of adolescent and

adult male chimpanzees have been well documented, the relationships between adolescent males themselves remain unclear. Specifically, prior studies have produced conflicting findings regarding whether adolescent males establish decided dominance relationships with their peers.

In the first detailed description of dominance relationships between wild male chimpanzees, Bygott (1979) found that subadults at the Gombe National Park did not form a rank hierarchy with each other. He noted: “Although immature males pant-grunted to adult males, they were not seen to pant-grunt to one another” (Bygott 1979: 414). Similarly, Hayaki and colleagues (1989) found that adolescent males in the Mahale Mountains National Park rarely pant grunted to each other. Pant grunts were also exchanged infrequently between adults. Of the relatively few that were given, most were directed to the alpha male. The paucity of data made it difficult to determine dominance relationships between some adult males, and the dominance relationships between adolescents could not be specified at all (Hayaki et al. 1989). Additional study at Gombe indicated that one 13-year-old adolescent male there behaved aggressively to an adult male, receiving pant grunts from him in the process (Pusey 1990). Nevertheless, dominance relationships between adolescents were not described, and a clear hierarchy involving them did not appear to exist.

In contrast to prior findings from Gombe and Mahale, Sherrow (2012) found that adolescent males at Ngogo in the Kibale National Park establish decided dominance relationships. Sherrow (2012) recorded 99 pant grunts between adolescent males and was able to construct a linear dominance hierarchy involving them. Because the Ngogo chimpanzee community is quite large compared to other chimpanzee groups, it is possible that demographic conditions created a highly competitive environment, leading adolescent males to form a dominance hierarchy to manage potentially high levels of aggression.

A different explanation for the finding that adolescent males at Ngogo form a dominance hierarchy emerges from analysis of long-term demographic records there and a reconsideration of male ages (Wood et al. 2016). Continuous observations of the Ngogo chimpanzees began in 1995 (Watts 2012). When Sherrow started his study in 2000, he therefore lacked information regarding the precise ages of his adolescent male subjects. Instead, as is the case in all other field studies of chimpanzees, male ages were initially estimated. Recently, age estimates of the chimpanzees at Ngogo have been reassessed and refined, using pedigree and genetic data (Wood et al. 2016). Applying these adjusted age estimates to Sherrow's sample indicates that nine of the 17 males he considered adolescents are likely to have been young adults during most of his study (Table 2.1). Thus, the finding that adolescent males at Ngogo form a dominance hierarchy may have been an artifact of including young adults in the sample.

To address the contradictory findings reported in prior studies regarding adolescent male chimpanzee dominance relationships, we conducted a follow-up study of dominance and aggression between adolescent males at Ngogo in the Kibale National Park, Uganda. We followed adolescent males in the same community of chimpanzees observed earlier by Sherrow (2008, 2012). We collected observations, however, 10 years after Sherrow did, and thus followed an entirely new cohort of adolescent males, whose birth dates are known to within 1 month to 1 year. Using this new sample of males allowed us to test the hypothesis that inaccurate age estimates may have created a false impression that clear dominance relationships exist between adolescent males at Ngogo in contrast to other chimpanzee communities.

METHODS

Study site and subjects

We conducted observations of adolescent male chimpanzees at Ngogo, Kibale National Park, Uganda, from August 2014 through August 2015. Ngogo lies at the center of the Park and is covered mostly by old growth rainforest interspersed by regenerating forest and grasslands (Struhsaker 1997). The Ngogo chimpanzees have not been provisioned by humans, and their territory is surrounded on all sides by other chimpanzee communities.

The chimpanzees at Ngogo have been observed continuously for 21 years and are habituated to human presence (Mitani 2009). The Ngogo chimpanzee community is extremely large. For most of the study period, it consisted of 193 individuals, including 31 adult males, 23 adolescent males, 63 adult females, 15 adolescent females, 10 juvenile males, 5 juvenile females, and 46 infants. As we conducted this study, some changes in the age-sex class composition of the community occurred due to births, deaths, and immigration.

Our subjects included 11 early adolescents (8-10 years old), 5 middle adolescents (11-13 years old), and 7 late adolescents (14-16 years old). One male (Barron) turned 14 years old during the course of the study and was considered a late adolescent thereafter. These age categories correspond to physical and social milestones in male chimpanzee development and are based on previous studies conducted on chimpanzees at the Gombe National Park, the Mahale Mountains National Park, and Ngogo (Goodall 1983; Goodall 1986; Kawanaka 1989; Sherrow 2008). Early adolescents have enlarged testicles relative to juveniles but are about half the size of adults; they spend most of their time traveling with their mother. Middle adolescents are larger than early adolescents, have pronounced testicles, spend variable time with their mothers, and are

still growing. Late adolescents are similar in height but slimmer than adult males. Late adolescent males spend a majority of their time away from their mothers. Exactly when male chimpanzees transition from adolescence to adulthood is not easy to discern. In the past, chimpanzee researchers have relied on chronological age to distinguish the two types of males, often considering males older than 15 years to be adults (Boesch and Boesch-Achermann 2000; Goodall 1983; Goodall 1986; Nishida et al. 2003; Reynolds 2005; Sugiyama 2004). While age and physical size undoubtedly change in tandem as males mature and make the transition to adulthood, their social behavior also undergoes profound transformation. Unlike adolescent males, adult male chimpanzees are fully integrated into the social network of other adults in the community (Goodall 1986). Because the 15- and 16-year old males in this study were not well integrated into the social world of prime adult males (Sandel, unpublished data), we considered them to be late adolescents instead of adults. While this age cut-off to demarcate adulthood differs from that used by some other chimpanzee researchers (Muller and Wrangham 2004b; Wroblewski et al. 2009), it is consistent with the one employed in the previous study at Ngogo (Sherrow 2008; Sherrow 2012), whose results we re-examine in this paper.

In all studies of wild animals, the ages of individuals born before the initiation of continuous long-term observation are estimates. At Ngogo, continuous study of adult males began in 1995. Detailed observations of adult females, who are the mothers of our subjects, were initiated in 2003. Thus, most of our subjects, who were adolescents in 2014, were identified in infancy, and their birth dates are known to within 1 month to 1 year. When the exact date of birth of males was unknown, they were assigned a birthdate on the first or fifteenth of the month, depending on when they were first observed during the month.

Behavioral observations

We collected observations of male pant grunts and aggressive behavior via focal and *ad libitum* sampling (Altmann 1974). Pant grunts are distinctive and easily recognizable calls that are directed up the dominance hierarchy given by low-ranking chimpanzees to higher-ranking individuals (Bygott 1979; De Waal 1982; De Waal and Van Hooff 1981). We recorded two types of aggression, contact and non-contact. Contact aggression included hitting, slapping, kicking, and biting. Non-contact aggression included four types of behavior: (1) Displays occurred when a male ran within 5 meters of another individual. Displaying males were often piloerect and dragged branches behind them; (2) Charges involved males running directly toward another individual instead of past them as in displays; (3) Chases were recorded when a male ran directly toward another individual and continued to run after victims as they moved away; (4) Other forms of agonism constituted a fourth class of non-contact aggression. Behaviors in this category included shaking branches and swatting an arm abruptly at another individual. When non-contact aggression escalated to contact aggression, we scored the aggressive event as contact aggression.

We recorded pant grunts and aggression between chimpanzees as they occurred. Sometimes a chimpanzee would approach a group of others pant grunting in the process. Other times, an individual might charge into another group of chimpanzees. In both cases, the recipients of pant grunts and aggression are unclear. For purposes of the following analyses, we included only pant grunts and aggression whose targets were unambiguous. Our use of *ad libitum* observations was predicated on the fact that the behaviors of interest, pant grunts and aggression, are rare yet conspicuous (Hayaki et al. 1989).

We followed chimpanzees from approximately 7:30 AM – 6:00 PM daily. We noted which individuals were visible at approximately 30-minute intervals to quantify contact time

with chimpanzees from whom pant grunts and aggression were recorded. If we had seen an individual within 14 minutes of the 30-minute interval, we recorded them as present at that time (e.g. if Booker was observed at 11:37 we recorded him as present at 11:30; if we observed him at 11:46, we recorded him as present at 12:00). Based on contact time with chimpanzees, A.A.S. observed them during 2,300 hours, including early adolescents (total hours/individual \pm SD: 61 ± 29.7 hours), middle adolescents (total hours/individual \pm SD: 135.6 ± 65.7 hours), and late adolescents (total hours/individual \pm SD: 146.8 ± 50.5 hours). R.B.R. observed chimpanzees during 800 hours, including early adolescents (total hours/individual \pm SD: 25.6 ± 11.8 hours), middle adolescents (total hours/individual \pm SD: 49.2 ± 23.2 hours), and late adolescents (total hours/individual \pm SD: 42.9 ± 14.7 hours).

Data collected via *ad libitum* sampling were supplemented with additional observations recorded during focal animal sampling (Altmann 1974). These consisted of hour-long following episodes in which we recorded social behaviors, including pant grunts and aggression. These focal samples were distinct from and in addition to “contact time” hours of observation. A.A.S. followed chimpanzees during 431 hours of focal observations between August 2014 and August 2015. Focal following episodes included observations of 3 middle adolescents and 7 late adolescents (total hours/individual \pm SD: 43.1 ± 3.1 hours). R.B.R. followed males during 155 focal hours between June and August 2015. Subjects included 9 early adolescents, 4 middle adolescents, and 7 late adolescents (total hours/individual \pm SD: 7.7 ± 2.2 hours; Online Resource 1). During two months, A.A.S and R.B.R. conducted observations concurrently, and for the most part, independently. A few times, however, they observed the same subject simultaneously. This created some overlap in contact time and focal hours of observation, leading to a slight overestimate in total hours of observation. Nevertheless, we guarded against

the possibility of inflating our behavioral observations of pant grunts and aggressive acts by carefully reviewing our data and counting cases in which both observers recorded the same pant grunt or aggressive act only once.

Statistical analyses

We tallied all instances of pant grunts and aggression given to and received by other adolescents. We entered these values into two separate interaction matrices, one for pant grunts (Table 2.2) and another for aggression (Table 2.3). To assess whether adolescents form a linear dominance hierarchy, we calculated de Vries (1995) improved test of linearity (h'), which is based on Landau's h , using DomiCalc (Schmid and de Vries 2013) in Microsoft Excel. This measure of linearity ranges from 0, indicating a non-linear hierarchy, to 1, indicating a completely linear, or transitive hierarchy (de Vries 1995; Schmid and de Vries 2013). To assess significance, we performed 10,000 randomizations of the linearity test, which generated a random linearity index, h_r . We compared h_r to the test statistic, h_o , which is equivalent to h' , the unbiased estimate for Landau's h (Schmid and de Vries 2013). If the probability of $h_r \geq h_o$ is less than 0.05, the hierarchy is considered significantly linear. More details regarding the calculation of h' and the test of linearity can be found in the handbook for DomiCalc (V. S. Schmid) (Schmid and de Vries 2013).

RESULTS

We recorded 857 pant grunts between males of all ages. Only 21 (2.5%) of these were exchanged between adolescent males. Most pant grunts were given by adolescent males to adults

(N = 569). Adolescent male chimpanzees received very few pant grunts. Early adolescents (8-10 years old, N = 11) and middle adolescents (11-13 years old, N = 5) never received pant grunts (Figure 1A). Six of the seven late adolescents (14-16 years old) received pant grunts from 1-4 individuals, and these tended to be pant grunts from much younger adolescent males (mean difference in age \pm SD = 4.8 ± 2.02 years younger; range = 7.4 younger to 0 years older; Figure 1A). Based on pant grunts, only 5.5% of adolescent male dyads had decided relationships (14/253 dyads). There was no indication of a linear hierarchy ($h' = 0.132$; $P = 0.458$). These results contrast with the pattern between adults. Although adult males were not the focus of our study, we recorded 265 pant grunts between adult males 17 years and older. Only 24% of all adult male dyads exhibited decided relationships (104/435), but there was a linear hierarchy ($h' = 0.221$; $P = 0.002$).

One late adolescent, Abrams, (15.5 years old) received a pant grunt from a low-ranking young adult male (Hawkins, 20.5 years old). This was the only time that an adolescent male received a pant grunt from an older chimpanzee. The dominance relationship between Abrams and Hawkins appeared to be in flux, as Abrams had pant grunted to Hawkins earlier in the year. Adolescent males who belonged to the same age-class exchanged pant grunts two times. Both cases involved one late adolescent (Wilson, 15.5 years old), who received pant grunts from two other late adolescents (Abrams, 15.5 years old and Barron, 14.3 years old). All other pant grunts received by late adolescents were given by males who were early adolescents or, on one occasion, a middle adolescent (Table 2.2). Half of the adolescent males (N = 13) were never observed pant grunting to other adolescents (Table 2.2). In sum, male chimpanzees did not receive pant grunts until late adolescence.

Like pant grunts, aggressive interactions between adolescent males were also rare, accounting for 10% of all aggressive acts observed between male chimpanzees of all ages. We recorded 502 cases of male-male aggression but only recorded adolescent males behaving aggressively with each other 51 times. Most of these cases involved non-contact aggression (47/51 times), including displays, charges, and chases. We recorded contact aggression, involving hitting, slapping, and kicking, only four times. Based on aggression, only 14.2% of dyads had decided relationships (36/253 dyads), and there was no linear hierarchy ($h' = 0.163$, $P = 0.247$). Combining aggression and pant grunts into one matrix produced similar results. Only 16.2% of all adolescent male dyads exhibited decided relationships (41/253), and there was no evidence of a linear hierarchy ($h' = 0.175$, $P = 0.186$).

Early adolescent males directed aggression toward other adolescents only three times (Figure 2.1B and Table 2.3). One event involved charging, and two involved one male shaking branches at another. Early adolescent males were victims in all three cases. Middle adolescents were aggressors six times. A middle adolescent charged another middle adolescent once. The five other occasions involved a middle adolescent behaving aggressively toward an early adolescent. One of the latter events resulted in contact aggression when Erroll (age 13.3 years) hit Orff (age 10.4 years) with a branch after Orff interrupted Erroll mating with an adolescent female. The remaining 42 cases of aggression involved late adolescents as aggressors. Seventeen of these aggressive events were single acts of aggression, but four late adolescents engaged in aggression more than once with the same adolescent. These involved ten dyads in 24 acts. Aggression was unidirectional across dyads, with one exception. Wilson, a late adolescent, charged and displayed at Lovano, another late adolescent, once. Lovano chased Wilson another time.

Adolescents tended to direct aggression toward individuals who were younger than themselves (mean difference in age \pm SD = 3.35 ± 2.52 years younger; range = 7.4 years younger to 0.9 years older). These acts exclude cases where adolescent males behaved aggressively toward adult males, which occurred 13 times. One of these instances involved a middle adolescent, Booker (age 13.1 years) displaying at a very small, low-ranking, and old adult male (Dizzy). All other instances involved late adolescents, including five individuals whose mean age was 14.9 years. Wilson accounted for five of these aggressive acts, and Abrams was the aggressor four times. The recipients of aggression were either young adults or very low ranking adult males, including two individuals with chronic injuries due to snares.

DISCUSSION

Given the absence of pant grunts received by early and middle adolescents, the paucity of pant grunts exchanged between late adolescents, the infrequent occurrence of adolescent-to-adolescent aggression, and the absence of a linear dominance hierarchy, it is reasonable to conclude that adolescent male chimpanzees at Ngogo do not display decided dominance relationships. These findings contrast with the patterns displayed between adult males, who pant grunted to each other more often than did adolescent males and who, unlike adolescents, formed a linear dominance hierarchy.

Aggressive interactions between adolescents occurred more often than the exchange of pant grunts, but were nonetheless still relatively rare. Most aggressive acts were given by late adolescents to early adolescents. Only at age 15 years did some males begin to dominate other adolescents to whom they were close in age. This is the same time that male chimpanzees

typically attempt to integrate themselves into the adult male dominance hierarchy by starting to behave aggressively toward low-ranking adult males (Nishida 2012; Pusey 1990).

Most pant grunts (17/21 = 81%) were given to males who were 15 and 16 years old. We were liberal in classifying these males as adolescents following precedents set earlier by Goodall (1983) and Sherrow (2008, 2012). Nevertheless, the possibility exists that these individuals had crossed the threshold to adulthood, as other chimpanzee researchers consider them to have done so (Muller and Wrangham 2004a). But if we adopted the criterion employed by some, an age cut-off of 14 years old and younger to define adolescence (Muller and Wrangham 2004a; Nishida 1997), we would have recorded even fewer pant grunt exchanges between adolescent males, only 4 times. Taken together, these observations indicate that adolescent males at Ngogo, like adolescent male chimpanzees elsewhere, do not form decided dominance relationships with their male peers.

Adolescent male chimpanzees pant grunt to one another at Gombe and Mahale only very rarely or not at all (Bygott 1979; Hayaki et al. 1989). These findings and our own, differ from Sherrow's (2012) previous observations at Ngogo. Sherrow (2012) reported that adolescent males there display decided dominance relationships and form a linear dominance hierarchy. Sherrow recorded 99 pant grunts between adolescents during 15 months of study between 2000 and 2004. This count far exceeds the 21 calls we observed in 12 months of study between 2014 and 2015. These observations leave us with an obvious and unresolved question: what explains these different findings?

As noted in the Introduction, there were pronounced differences in the way the ages of male subjects were determined in this study and in Sherrow's (2008, 2012) earlier work, and this likely contributed to our discrepant findings. Sherrow began his research only five years after

long-term observations commenced at Ngogo. At that time, the adolescent males were difficult to observe on the ground, and their ages were estimated using their physical appearance and behavior (Sherrow 2008). Over the past 15 years, the ages of all individuals have been reassessed using pedigree and genetic data and observations of the developmental trajectories of males of known ages (Wood et al. 2016). Using these revised estimates, nine of Sherrow's 17 subjects were likely to have been young adults, 17 years old and older, rather than adolescents during the majority of his study. In contrast, our male subjects were first observed as infants and juveniles, and their ages can be estimated to the nearest month or year. While it is impossible to know with certainty the ages of the young males observed by Sherrow, we can say with confidence that the adolescents we observed were adolescents and that they do not form a dominance hierarchy with their peers.

Our observations that late adolescent males receive pant grunts and give aggression more often than do younger males are suggestive of an age-based hierarchy. While this possibility exists, it is impossible to evaluate in the absence of additional data on dominance interactions between adolescent males. The paucity of data in this regard may be due to the fact that we followed early adolescent males as focal subjects over a relatively short period and only a few times (56 focal hours over 3 months). The results that we have reported here should be considered with this in mind. We did have considerable contact time with early adolescents (732 hours over 12 months by A.A.S. and 307 hours over 3 months by R.B.R), but our *ad libitum* observations may have missed instances of aggression involving them. Nevertheless, the fact remains that we observed adolescent males pant grunting to other adolescent males only a very few times. In addition, our observations of an extremely large cohort of middle and late adolescent males provide no hint of an adult-like hierarchy among the older adolescents.

Another issue that we did not address specifically involves variation in opportunities for adolescents to interact. Given the fission-fusion nature of chimpanzee communities, some individuals associate more than others (Goodall 1986; Mitani and Amstler 2003; Newton-Fisher 1999; Nishida 1968; Pepper et al. 1999). This is especially true of adolescents, who do not range as widely within the territory as do adult males. In the present analysis, we did not account for “structural zeros,” or the absence of dominance interactions due to a lack of opportunities to interact (de Vries 1995). We do not suspect that an absence of opportunities influenced our results, as most adolescent males had ample chances to exchange calls and engage in aggression. The majority of dyads (236/253) associated with one another, but males in these pairs rarely pant grunted to each other, and clear dominance relationships between them were impossible to discern. Given this, the formal analysis of linearity that we performed (de Vries 1995; Schmid and de Vries 2013) yielded a predictable null result and provides a stark contrast to the findings from the previous study at Ngogo (Sherrow 2012). In sum, further investigation of early and middle adolescent aggressive behavior and dominance relationships is required. Until then, the preponderance of current evidence indicates that adolescent male chimpanzees do not form a dominance hierarchy with their peers.

The finding that adolescent male chimpanzees do not establish decided dominance relationships between themselves may be surprising given the importance of rank in adulthood and the fact that other primates form dominance relationships during adolescence. Why do male chimpanzees wait until adulthood? The prolonged time it takes male chimpanzees to form dominance relationships with others in their community represents one possibility. Male chimpanzees begin the process of establishing rank by behaving aggressively toward and attempting to dominate adult females (Nishida 2003; Pusey 1990). This takes time and involves

nontrivial effort because adult females retaliate with aggression and are able to rebuff their challenges, at least initially (Nishida 2012; Pusey 1990). As a consequence, male chimpanzees are able to achieve dominance over adult females only toward the end of adolescence (Goodall 1986; Pusey 1990). They then start to compete with their peers, but by this time, they have already crossed the threshold to adulthood.

Adult male behavior is a second factor that might limit and constrain aggression and competition between adolescent male chimpanzees. Here, adolescent males may avoid aggression with peers as this can lead to retaliation by adults. Although we did not quantify it, on some occasions higher-ranking adults attacked adolescent and young adult males after the latter behaved aggressively. Consequently, adolescents may benefit by remaining under the radar of adult males. It is only after they have reached physical and social maturity in adulthood that male chimpanzees are able to compete effectively with conspecifics, and this may be the time that they switch gears and start to strive for status and attempt to dominate their peers.

A third possibility is that adolescent males prioritize forming social bonds over competing with each other. Male chimpanzees are philopatric, and to reproduce they must integrate themselves into the social network of adult males. Consequently, their effort might be better spent on developing affiliative rather than agonistic relationships with peers, as cooperative bonds in adulthood translate into fitness benefits (Gilby et al. 2013; Mitani 2009; Watts and Mitani 2001). To date, few studies have investigated the development of social bonds in adolescent male chimpanzees (Kawanaka 1989; Kawanaka 1993; Pusey 1990). Whether adolescents form social bonds with their peers remains an open question and requires additional research.

Although adolescent male chimpanzees do not vie for status with their peers, aggressive encounters between adolescents may still be important for future dominance relations. Juveniles and early adolescents engage in aggressive interactions occasionally (Markham et al. 2015), and in captivity, adolescents display dominance in the context of play (Paquette 1994). Although distinct from adult dominance relationships, juvenile play may be important practice and have an impact later in adulthood. For example, juvenile marmot play patterns predicted adult dominance relationships (Blumstein et al. 2013). Given that it takes male chimpanzees a long time to grow up, the social behaviors exhibited during juvenility and adolescence may have important consequences in adult life.

In sum, our finding that adolescent male chimpanzees do not establish dominance relationships with their peers is surprising given the importance of rank in adult male chimpanzee life. It is also perplexing because dominance appears to manifest during adolescence in other primates, including humans (Pellegrini 2002; Savin-Williams 1979). The three hypotheses that we have proposed above require testing. Given the fundamental importance of understanding the development of behavior (Tinbergen 1963), these tests, along with additional studies of chimpanzee adolescence and ontogeny, remain a high priority for future research.

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Table 2.1. Male chimpanzees observed in a previous study at Ngogo. The age class of male subjects and their ranks are shown as reported in Sherrow (2012). Updated age estimates used in this study are also listed. Males whose age estimates are not the same are indicated in bold.

Name	Code	Rank ^a	Age category ^a	Age category updated (2003-2004) ^b	Est. DOB ^b	Age Aug 2000 ^b	Age Dec 2004 ^b
Dexter ^{c,d}	DX	1	Late adolescent	Young adult	1985	15.6	19.9
Getz ^c	GZ	2	Late adolescent	Young adult	1986	14.6	18.9
Rahsaan ^c	RN	3	Late adolescent	Young adult	1987	13.6	17.9
Webster ^{c,d}	WB	4	Late adolescent	Late adolescent	1988	12.6	16.9
Tatum ^{c,d}	TA	5	Late adolescent	Young adult	1986	14.6	18.9
Rollins ^c	RO	6	Late adolescent	Young adult	1986	14.6	18.9
Branford ^{c,d}	BD	7	Late adolescent	Young adult	1987	13.6	17.9
Richmond ^{c,d,e}	RI	8	Late adolescent	Young adult	1987	13.6	17.9
Carter ^c	CA	9	Mid adolescent	Mid adolescent	1990	10.6	14.9
Mulligan ^c	MU	10	Mid adolescent	Late adolescent	1989	11.6	15.9
Garrett ^{c,d}	GT	11	Mid adolescent	Late adolescent	1989	11.6	15.9
Waller ^{c,e}	WA	12	Late adolescent	(Young) adult	1982	18.6	22.9
Satchmo ^c	SA	13	Early adolescent	Young adult	1987	13.6	17.9
Jackson ^f	JA	14	Early adolescent	Mid adolescent	1991	9.6	13.9
Cash ^c	CS	15	Early adolescent	Early adolescent	1993	7.6	11.9
Southpaw ^c	SP	16	Early adolescent	Early adolescent	1993	7.6	11.9
Herbie ^c	HH	17	Early adolescent	Early adolescent	1994	6.6	10.9

^aBased on Sherrow (2008, 2012); ^bBased on current consensus among current directors of Ngogo Chimpanzee Project (Kevin Langergraber, John Mitani, David Watts); birthdate assigned to the first of January of the estimated year of birth; ^cEstimated based on physical appearance compared to chimpanzees of estimated age at the time and known age retrospectively; ^dEstimated based on older sibling; ^eEstimated based on younger sibling; ^fEstimated based on physical appearance compared to chimpanzees of known age

Figure 2.1. Dominance rank interactions between adolescent male chimpanzees (8 to 16 years old). (a) Pant grunts. The age of callers (subordinate individuals) is plotted vs. the age of recipients (dominant individuals). (b) The age of recipients of aggression (subordinate individuals) is plotted versus the age of aggressors (dominant individuals). Interactions between males of different ages are denoted by semi-transparent grey dots, with darker dots representing overlaid data points, e.g. the dot at (9, 14.5) in 2.1A appears dark because 9-year-old males pant-grunted to 14.5-year-old individuals multiple times.

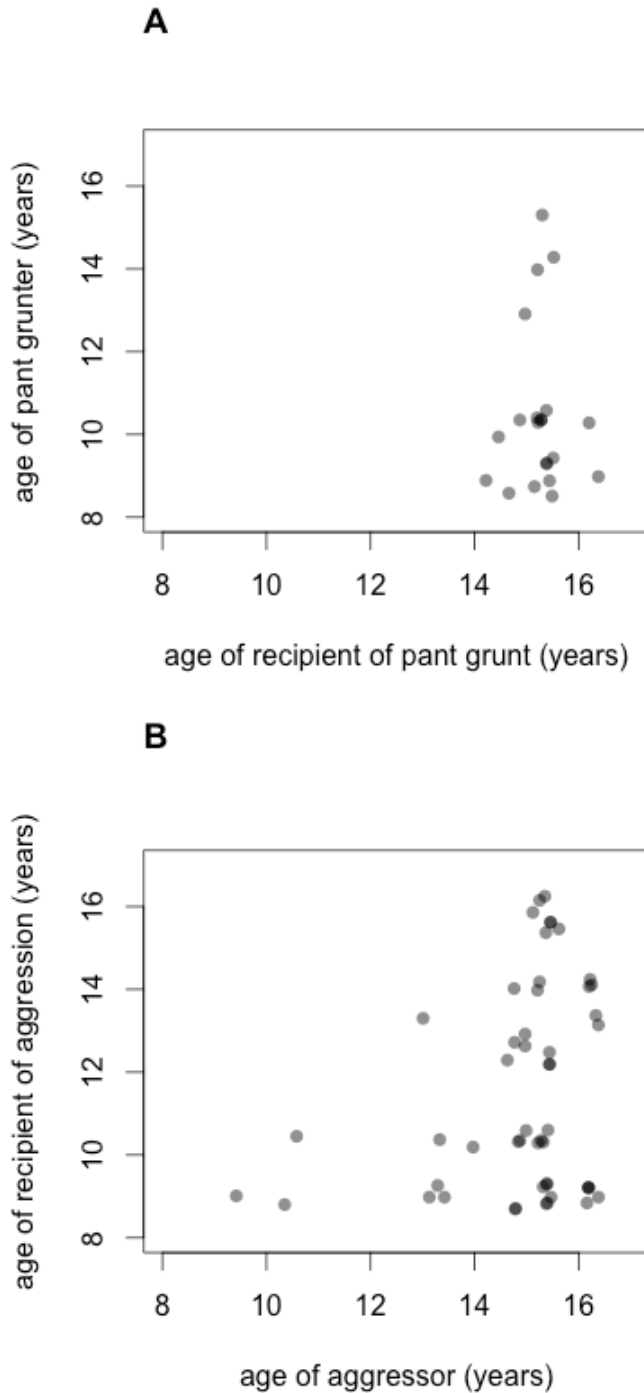


Table 2.2. Pant grunt matrix for adolescent males. Individuals are ordered by age (years). Ages reported in the table are based on age at the midpoint of study (February 1, 2015). Pant grunts are shaded. Zero in parentheses indicate individuals that were never observed in the same subgroup and thus had no opportunity to interact. Dashed line separates late adolescents from middle and early adolescents. Solid line separates males who some researchers would consider adults (15 years and older).

Recipient age	16.1	16.1	15.4	15.2	15.2	15.1	14.7	14.1	14.0	13.1	12.8	12.1	10.3	10.1	10.1	10.1	10.1	10.1	9.1	9.1	9.0	8.7	8.6	8.6	Sum pant grunts received	
Caller age	16.1	16.1	15.4	15.2	15.2	15.1	14.7	14.1	14.0	13.1	12.8	12.1	10.3	10.1	10.1	10.1	10.1	10.1	9.1	9.1	9.0	8.7	8.6	8.6	Sum pant grunts given	
	Haden	Mitchell	Lovano	Abrams	Wilson	Buckner	Benny	Chopin	Barron	Erroll	Booker	Bosko	Murray	BillyBragg	Elton	Jarman	Orff	Powell	YoYo	PeaWee	Fleck	Damian	Dylan			
16.1	Haden	0	0	0	0	0	0	0	0	0	0	0	0	(0)	0	0	0	0	0	0	0	0	0	0	1	
16.1	Mitchell	0	*	0	0	0	0	0	0	0	0	0	(0)	0	0	0	0	0	0	0	0	0	0	0	0	2
15.4	Lovano	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.2	Abrams	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
15.2	Wilson	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
15.1	Buckner	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
14.7	Benny	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
14.1	Chopin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14.0	Barron	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13.1	Erroll	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
12.8	Booker	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12.1	Bosko	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10.3	Murray	0	(0)	0	0	0	0	0	0	0	0	0	*	0	0	0	0	0	0	0	0	0	0	0	0	0
10.1	BillyBragg	(0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10.1	Elton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10.1	Jarman	0	0	0	0	0	0	0	0	0	0	0	(0)	0	0	0	0	0	0	0	0	0	0	0	0	0
10.1	Orff	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.1	Powell	0	(0)	0	0	0	0	0	0	0	0	0	(0)	0	0	0	0	0	0	0	0	0	0	0	0	0
9.1	YoYo	(0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.0	PeaWee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.7	Fleck	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.6	Damian	0	(0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.6	Dylan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sum pant grunts given	0	0	0	1	0	0	0	0	2	1	0	0	2	4	0	1	1	1	0	0	5	0	2	2	2	

Table 2.3. Aggression matrix for adolescent males. Individuals are ordered by age (years). Ages reported in the table are based on age at the midpoint of study (February 1, 2015). Aggressive events are shaded. Zero in parentheses indicate individuals that were never observed in the same subgroup and thus had no opportunity to interact. Solid line separates males who some researchers would consider adults (15 years and older).

Aggressor age	Recipient age	16.1	16.1	15.4	15.2	15.2	15.1	14.7	14.1	14.0	13.1	12.8	12.1	10.3	10.1	10.1	10.1	10.1	10.1	9.1	9.1	9.0	8.7	8.6	8.6	8.6	Sum aggression given		
		Haden	Mitchell	Lovano	Abrams	Wilson	Buckner	Benny	Chopin	Barron	Erroll	Booker	Booko	Murray	BillyBragg	Elton	Jarman	Off	Powell	YoYo	PeeWee	Fleck	Damien	Dylan					
16.1	Haden	*																											
16.1	Mitchell	0	*																										
15.4	Lovano	0	0	*																									
15.2	Abrams	0	0	0	*																								
15.2	Wilson	0	0	0	0	*																							
15.1	Buckner	0	0	0	0	0	*																						
14.7	Benny	0	0	0	0	0	0	*																					
14.1	Chopin	0	0	0	0	0	0	0	*																				
14.0	Barron	0	0	0	0	0	0	0	0	*																			
13.1	Erroll	0	0	0	0	0	0	0	0	0	*																		
12.8	Booker	0	0	0	0	0	0	0	0	0	0	*																	
12.1	Booko	0	0	0	0	0	0	0	0	0	0	0	*																
10.3	Murray	0	0	0	0	0	0	0	0	0	0	0	0	0	*														
10.1	BillyBragg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*													
10.1	Elton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*												
10.1	Jarman	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*											
10.1	Off	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*										
9.1	Powell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*								
9.1	YoYo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.0	PeeWee	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.7	Fleck	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.6	Damien	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.6	Dylan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sum aggression received	3	0	0	2	1	1	0	2	4	5	4	1	2	5	0	1	2	0	0	0	0	0	0	0	0	3		

CHAPTER 3

Social bonds with fathers, brothers, and others during the transition to adulthood in male chimpanzees

ABSTRACT

Social bonds are important for many animals. Bonds with kin provide inclusive fitness benefits, and those within non-kin provide direct benefits through cooperation. Adult male chimpanzees (*Pan troglodytes*) exhibit social bonds with maternal brothers as well as unrelated adult males, which facilitate high dominance rank. It is unknown when social bonds between males develop. Prior studies hint that social bonds emerge during adolescence, but bonds may develop during adulthood when male chimpanzees begin competing for dominance status. To investigate these possibilities, we studied the social relationships of adolescent and young adult male chimpanzees at Ngogo in Kibale National Park, Uganda. Adolescent male chimpanzees formed social bonds with other males, and they did so as often as did young adult males. Adolescent and young adult males frequently joined subgroups with old males. They spent time in proximity to and grooming with old males, although they also did so with their age peers. Controlling for age and age difference, males formed strong association and proximity relationships with their maternal brothers and grooming relationships with their fathers. Grooming bonds between chimpanzee fathers and their adolescent and young adult sons have never before been documented and are unexpected because chimpanzees mate promiscuously.

How fathers recognize their sons and vice versa remain unclear, but may be due to familiarity from relationships earlier in development. The bonds forged between sons and fathers provide insights into the evolution of these relationships in humans.

INTRODUCTION

Social bonds play an important role in animal behavior (Massen et al. 2010; Seyfarth and Cheney 2012; Silk 2002). Female mammals who form strong social bonds have higher infant survivorship, live longer, and display lower stress levels than females who form weak bonds (Cameron et al. 2009; Crockford et al. 2008; Silk et al. 2009; Silk et al. 2010; Silk et al. 2003; Wittig et al. 2008). Male primates have also been shown to obtain fitness benefits by forging strong social bonds; male macaques who do so reproduce more than others who are unable to develop similar bonds (Schülke et al. 2010). Social bonds feature prominently in adult male chimpanzees (*Pan troglodytes*), who remain in their natal communities throughout their lives (Goodall 1986; Nishida 1979) and form social bonds with maternal half-brothers and non-relatives, especially individuals similar in age and rank (Langergraber et al. 2007; Mitani 2009b; Mitani et al. 2002). Males who forge bonds cooperate via short-term coalitions and long-term alliances that influence the acquisition and maintenance of high dominance rank (Nishida 1983; Nishida and Hosaka 1996), which is positively related to male reproduction (Boesch et al. 2006; Gilby et al. 2013; Langergraber et al. 2013; Newton-Fisher et al. 2010; Wroblewski et al. 2009).

While the ability of adult male chimpanzees to cultivate and maintain social bonds provides a competitive advantage in status competition and reproduction, exactly when social bonds develop remains unclear (Kawanaka 1989; Pusey 1990). Two possibilities exist. One possibility

is that they develop during adulthood because adolescents and younger individuals may not yet be in a position to derive important benefits by forming social bonds with others. As noted above, adult male chimpanzees forge social bonds with relatives and peers to help in the acquisition and maintenance of dominance rank (Nishida 1983; Riss and Goodall 1977). Adolescent male chimpanzees, however, do not form decided dominance relationships with their peers (Bygott 1979; Hayaki et al. 1989; Chapter 1). As a consequence, male chimpanzees may wait to establish bonds with others until adulthood, when they begin competing for status. In addition, adolescent males remain relatively asocial, spending considerable time alone and at the periphery of social gatherings (Kawanaka 1993; Pusey 1990). As a consequence, it may be difficult for them to forge social bonds until they become more gregarious during adulthood.

A second possibility is that social bonds form before adulthood, specifically during adolescence when male chimpanzees become fully independent of their mothers and start to integrate into the social world of adult male chimpanzees. During adolescence, male chimpanzees spend an increasing amount of time with adult males but remain socially peripheral, as they are frequent targets of aggression and rarely groomed (Kawanaka 1989; Pusey 1990; Sherrow 2008). To negotiate the difficult transition to adulthood, adolescents may form social bonds with conspecifics (Nishida 2012; Pusey 1990). Prior observations of four adolescent males at Gombe National Park, Tanzania, indicated that one preferentially traveled with an older brother, another did so with the alpha male, and a third did so with four unrelated males, including three old males (Pusey 1990). Similarly, three of seven adolescent male chimpanzees at Mahale Mountains National Park, Tanzania, spent considerable time in close spatial proximity to specific males (Kawanaka 1989). These observations furnish a tantalizing hint that adolescent

males form social bonds with others, but more data are necessary to confirm that this actually occurs.

If such bonds exist, additional research is also required to determine the factors that influence their formation. Qualitative observations made thus far suggest that adolescent males may seek the company and support of high-ranking and older males (Nishida 2012; Pusey 1990). Recent studies of immature chimpanzees and other primates also suggest that fathers and offspring interact with each other non-randomly (Charpentier et al. 2007; Charpentier et al. 2008; Godoy et al. 2016; Huchard et al. 2013; Langos et al. 2013; Lehmann et al. 2006; Murray et al. 2016; Pfefferle et al. 2014; Widdig 2007). In addition, previous research on adult male chimpanzees suggests that social bonds preferentially form between individuals who are similar in age and between maternal brothers, but not between paternal brothers (Langergraber et al. 2007; Mitani 2009b; Mitani et al. 2002). Whether similar factors influence bond formation in adolescents is unknown.

In this paper, we investigate the development of male chimpanzee social relationships during the transition to adulthood. To do so, we studied a large cohort of young male chimpanzees at Ngogo in Kibale National Park, Uganda. We observed ten adolescent chimpanzees ranging in age from 12 to 16 years, comparing the affiliative patterns of these adolescents to those of eight young adult males ranging in age from 17 to 21 years. We address two questions. First, do adolescent male chimpanzees form social bonds with other males or do bonds develop later after males reach adulthood? Second, what factors influence the formation of social bonds? Specifically, we examine the effects of age and kinship (i.e., maternal and paternal brothers and father-son pairs).

METHODS

Study Site and Subjects

We conducted observations of adolescent male chimpanzees at Ngogo, Kibale National Park, Uganda, over 12 months from August 2014 to August 2015. Located in the center of the park, the Ngogo study site is surrounded on all sides by other chimpanzee communities and is covered mostly by old growth rainforest interspersed between areas of regenerating forest and grasslands (Struhsaker 1997). The Ngogo chimpanzee community is large. For most of the study period, it consisted of 193 individuals, including 31 adult males, 23 adolescent males, 63 adult females, 15 adolescent females, 10 juvenile males, 5 juvenile females, and 46 infants. Subjects were ten middle and late adolescent males (12-16 years old) and eight young adult males (17-21 years old). These age categories correspond to physical and social milestones in male chimpanzee development and are based on previous studies conducted on chimpanzees at Gombe National Park and Mahale Mountains National Park in Tanzania and at Ngogo (Goodall 1983; Goodall 1986; Kawanaka 1989; Sherrow 2008; Chapter 1). Although adolescence in male chimpanzees commences around 8 to 10 years of age, when their testes start to enlarge, we restricted study to individuals who had reached middle and late adolescence, as this is the time males begin to travel independently from their mothers on a regular basis (Pusey 1983; Pusey 1990). Goodall (1983: 4) notes: “In behavioural terms, some males may not reach social maturity until 16 or even 17 years old.” Because the two 16-year-old males in our sample were not involved in dominance interactions with their peers (Chapter 1), we classified them as adolescents.

Behavioral Observations

One of us collected observations of male social behavior via continuous focal animal sampling (Altmann 1974). He followed chimpanzees from approximately 0730 – 1800 daily. Following episodes lasted 1 hour during which he recorded grooming continuously, timing to the nearest second who groomed whom. The time that subjects were out of sight was also noted, and only following episodes with at least 40 minutes of continuous observation were included to guard against the potential bias of exaggerating the significance of behaviors that occurred over short periods. The identity of all adolescent and adult males over 8 years of age that were in proximity (≤ 5 m away) to the focal subject was recorded every 10 minutes. Chimpanzee societies have high fission-fusion dynamics, where community members are rarely or never all found together in the same place at the same time, but instead associate in temporary parties that vary in size, composition and duration (Goodall 1986; Nishida 1968; Nishida 1979). All adolescent and adult males that the focal subject encountered (i.e. were in visual range) during the hour-long following episode were considered in association (cf. Mitani et al. 2002). We used a data collection program (HanDBase[®] by DDH Software) on a hand-held electronic device (iPhone 5), which automatically recorded the time and duration of observations. Because chimpanzees live in fission-fusion societies, not all males were available for observation every day. We equalized the number of focal follows by rotating through subjects on an opportunistic basis, prioritizing males who had been observed less often than others. We conducted 812 total following episodes representing 773.5 hours of observation (mean hours/individual \pm SD: 43.1 ± 3.1 hours, range = 38 to 50 hours, N = 18 males).

Assessing Social Bonds

Chimpanzee social relationships and the bonds that exist between individuals are manifest in three behaviors: association, proximity, and grooming. Patterns of association result from individual social decisions that presumably reflect who prefers to be with whom (Newton-Fisher 2002). We computed dyadic association by dividing the number of following episodes during which pairs of males were together by the number of times the focal subject was followed. As they associate with others in parties, chimpanzees spend time in close spatial proximity to certain individuals, which provides another indication of partner preference. Dyadic proximity was calculated as the number of scan samples in which pairs of males were ≤ 5 m apart, divided by the total number of scan samples for the focal subject. Finally, grooming is frequently used to assay social bonds between primates (Dunbar 2010; Silk et al. 2013), including male chimpanzees, who typically groom a small subset of individuals (Mitani 2009b; Watts 2000). Dyadic grooming was calculated as the minutes pairs of males spent grooming, divided by the number of observation hours for the focal subject.

To assess social bonds between male chimpanzees, we analyzed associations, spatial proximity, and grooming interactions separately. While some researchers combine different affiliative behaviors into a single index (Sapolsky et al. 1997; Silk et al. 2006), each behavior may reflect different aspects of relationships (Hirsch et al. 2012; Schoof and Jack 2014), and combining them may not furnish an accurate depiction of the bonds between animals (Lehmann et al. 2007). In this study, association, proximity, and grooming were correlated with one another, but there was variability. Some pairs of males spent considerable time associating but not in proximity, while others spent time in proximity but not grooming.

There is no consensus on how to define social bonds between individuals (Dunbar and Shultz 2010; Silk et al. 2013; Silk 2002; Whitehead 2008). We measured social bonds based on: (1) the amount of time individuals spent together, either in association, proximity, or grooming, relative to other dyads in the sample (Schoof and Jack 2014; Silk et al. 2006) and (2) whether males consistently engaged in all three types of behavior (Smuts 1985; Whitehead 2008).

We began by assuming that young adult male chimpanzees, like older adults, form social bonds with other males (Langergraber et al. 2007; Mitani 2009b). We proceeded to determine which of the young adult males in our sample formed such bonds. We calculated the association frequencies, proximity frequencies, and grooming rates of young adult subjects with other adult males. Adult dyads that fell in the top 10% of values in the distributions of each of the three behaviors were considered to have social bonds, corresponding to the definition of bonded pairs used in prior studies (Silk et al. 2006). We then computed dyadic association, proximity, and grooming distributions for adolescent male subjects. We classified pairs of adolescents and other males whose values fell above the 10% cut-off points in the young adult samples as socially bonded. When constructing these distributions, we took the perspective of focal subjects, whether adolescent or young adults, and calculated dyadic association frequencies, proximity frequencies, and grooming rates from data collected while they were focal subjects. We included bonds formed between our 18 focal subjects and all adolescent and adult males ranging in age from 8 to over 50 years. Focal subjects could therefore appear as the partner of another adolescent or young adult in dyads. Because we took the perspective of the focal subject, when the focal subject was an adolescent and he formed a bond with a young adult, we classified the bond as one formed by an adolescent. Conversely, when the focal subject was a young adult and he formed a bond with an adolescent, we classified the bond as one formed by a young adult.

As a second means to assess social bonds, we determined whether pairs of males displayed bonds based on the three measures of social behavior (Whitehead 2008). If a pair displayed bonds in all three behaviors, they were defined as having a ‘triple bond.’ We consider triple-bonded males to possess strong social bonds.

Age

Detailed observations of adult female chimpanzees, who are the mothers of our subjects, were initiated in 2001 at Ngogo (Langergraber et al. 2009; Wakefield 2008). Thus, most of our subjects, who were adolescents and young adults in 2014, were identified as infants or juveniles, and their birth dates are known to within 1 month to 1 year (Wood et al. 2017; Chapter 1).

To assess the effect of age on the formation of social bonds, we created an age difference variable for each dyad by computing the absolute value of the difference between the age of the focal subject and the age of the other individual. We also assessed whether adolescent and young adult males formed triple bonds with males in different age classes. We considered males peers if they were within five years in age (Mitani 2009b). Each adolescent and adult male in the sample had an average of 20 peers ($SD = 2$), with peers represented in 359 dyads. We defined potential male partners as old if they were 35 years old or older (Moeller et al. 2016). Based on this criterion, there were eight old males (mean age \pm $SD = 43 \pm 5$ years, range = 38 to 53 years) in 144 dyads.

Kinship

Kin relationships between all of our subjects are known based on prior behavioral observations and genetic analyses of autosomal, X-chromosomal, and Y-chromosomal

microsatellite loci, and of mitochondrial DNA (Langergraber et al. 2007; Langergraber et al. 2013; Langergraber et al. 2009). Pairs of males were assigned as maternal brothers, paternal brothers, fathers and sons, or ‘unrelated’ (i.e, all other types of dyads, including distant relatives such as uncle-nephew and first cousins). Twelve adolescent and young adult males had maternal brothers who were adolescents or adults, representing 15 dyads. All maternal brothers were half-siblings except for one pair who were full siblings. Fourteen adolescent and young adult males had paternal brothers who were adolescents or adults, representing 34 dyads. This total excluded the full sibling pair, who we classified as maternal brothers for purposes of the following analyses. Eleven adolescent and young adult males had living fathers, who included six different males.

Statistical Analyses

To determine whether adolescent males formed social bonds with other adolescent or adult males as often as did young adults, we compared the mean number of bonds displayed by males of both age classes using a Welch unequal variance t-test. We used the number of times adolescents formed triple bonds with others as a second means to evaluate how frequently they developed bonds compared to young adults. Here we calculated the number of times adolescent males formed bonds based on all three behaviors divided by the total number of triple bonds formed by adolescent and young adult subjects. We used the resulting percentage as a test statistic. High values indicated that adolescents formed strong bonds frequently, while low values reflected the opposite. Because pairs were the unit of analysis, individuals appeared multiple times, and data points were not independent. In addition, there were ten adolescents and eight young adults in the sample, so the former had a higher probability of being in bonded pairs.

To generate a null distribution of the percentage of strong bonds formed by adolescents, we drew pairs of males at random without replacement from the pool of 954 total dyads, holding the observed number of triple bonds constant. We then calculated the number of times adolescents appeared in the samples of triple bonds relative to the total number of triple-bonded pairs, and used this as one datum in the null distribution. We repeated this process 10,000 times to generate a 95% confidence interval. We compared the observed test statistic to this confidence interval to evaluate whether adolescents formed strong bonds as frequently as did young adults.

To assess the effects of age, age difference, and kinship on the formation of social bonds by adolescent and young adult males, we conducted three generalized linear mixed models, with association, proximity, and grooming between pairs of males as the outcome variables. Fixed effects were the age of the adolescent or young adult subject, the dyads' kin relationship (i.e., maternal brothers, paternal brothers, father-son, or unrelated), the age of the other male, and the absolute value of the age difference between the pair. Association and proximity were kept as counts, while grooming was measured as a continuous variable, the duration of time spent grooming. For the association model, we added the log number of hour-long following episodes on the focal subject as a fixed effect to control for variation in observation time. In the proximity and grooming models, we excluded dyads that never associated and added the log number of times each pair was in association as a fixed effect to control for variation in opportunities to interact. The identities of subjects and the other individual in the dyad were included as two random effects. We set a negative binomial error distribution using the “lme4” package (Bates et al. 2015) in R (R Core Team 2015). We used a null-hypothesis testing framework to assess the importance of the fixed effects, and we report their coefficients and p -values.

In a final series of analyses, we calculated the percentage of triple bonds between adolescents and young adults and: 1) peers and old males, and 2) maternal brothers, paternal brothers, fathers, and unrelated males. We conducted the same randomization procedure described above to generate expected confidence intervals and used these to assess the effects of relatedness and age on the formation of bonds.

RESULTS

When do social bonds form?

Adolescent male chimpanzees formed social bonds (Figure 3.1), and they did so as frequently as did young adult males (Figure 3.2). The number of bonds based on associations did not differ between adolescents (mean \pm SD = 4.4 ± 3.5) and young adults (mean = 4.1 ± 3.6 , Welch two sample t-test: $t_{14,957} = 0.165$, $P = 0.872$) nor did the number of proximity bonds (adolescent mean \pm SD = 2.2 ± 2.3 , young adult mean \pm SD = 2.6 ± 1.7 , $t_{15,917} = -0.452$, $P = 0.657$) or grooming bonds (adolescent mean \pm SD = 2.2 ± 2.2 , young adult mean \pm SD = 3.0 ± 3.0 , $t_{12,452} = -0.627$, $P = 0.542$).

All adolescent males forged at least one type of social bond with another male. Nine of ten adolescents formed an association bond. Seven of ten adolescents exhibited proximity bonds and seven displayed grooming bonds. Only two adolescent males did not form proximity or grooming bonds (Figure 3.2). Adolescent males displayed 44 associations bonds, 22 proximity bonds, and 22 grooming bonds with other males. These values underestimate the true number of social bonds involving adolescents because bonds between them and young adults, calculated from when the latter were targets of observation, are not included in these totals. Of the 33

association bonds exhibited by young adults, 11 were with adolescent males. Most proximity (95.2% = 20/21) and grooming bonds (91.7% = 22/24) formed by young adults, however, were with adults rather than with adolescents.

By middle and late adolescence, male chimpanzees exhibit social relationships comparable to those of young adults. Some pairs of males formed particularly strong bonds based on the three different measures of behavior, and adolescents did so as frequently as did young adults.

Adolescents were involved in 70% (7/10) of triple bonds (95% confidence interval (CI) = 20 - 80%). In addition, the age of the subject did not predict the strength of association, proximity, or grooming relationships that adolescent and young adults formed with other males (Table 3.1).

Because adolescent and young adult males did not differ in the number or strength of bonds that they formed with others, we combined the two age groups in subsequent analyses to increase the power of statistical tests.

Effect of age and age difference

Adolescent and young adult males associated, spent time in proximity, and groomed more often with males as the age of their male partner increased (Table 3.1). Indeed, some of the strongest bonds involved the eight oldest adult males, who were 38 years and older. These males were involved in 40% of all of the triple bonds, a percentage that approached the outer bound of the 95% confidence interval (0 to 40%). These old males were also involved in 9 association bonds, 15 proximity bonds, and 16 grooming bonds.

Although adolescent and young adults frequently formed relationships with old males, some bonds did develop between peers. Controlling for the preference for old males, assessed through the greater frequency of interaction with males as their age increased, male subjects spent more

time in proximity to and grooming with others similar in age compared to males who were older or younger (Table 3.1). Peers were involved in 32 association bonds, 11 proximity bonds, and 11 grooming bonds. Several bonds between peers were particularly strong, with 30% of all triple bonds formed between peers. This percentage, however, fell within the bounds of the 95% confidence interval (10 to 70%). Taken together, these results indicate that adolescent and young adult males avoid younger adolescents as social partners in favor of peers and old males.

Effect of kinship

Controlling for age of the individuals and age difference between pairs, adolescent and young adult males were more likely to form bonds with individuals in some kin categories compared with unrelated males (Figure 3.3). Adolescent and young adult male subjects associated with and spent time in proximity to maternal brothers more often than they did with unrelated males (Table 3.1). Maternal brothers formed some of the strongest bonds with each other, displaying a significantly higher than expected number of triple bonds (30% of bonds; expected CI: 0 to 10%). Although maternal kinship had a strong effect on the formation of bonds, its effect was not uniform. Adolescent and young adults did not groom more frequently with their maternal brothers than with unrelated males (Table 3.1). In addition, seven of the 15 males failed to form any type of social bond with their maternal brothers. In four of these seven cases, adolescent and young adult males did not develop bonds with their younger adolescent brothers. In two cases they did not establish bonds with their high-ranking, prime adult brothers. Finally, one adolescent did not form a bond with his low-ranking, prime adult brother.

In contrast to maternal kinship, there was no preference to groom with, spend time in proximity to, or associate with paternal brothers (Table 3.1). There were no triple-bonded

paternal brothers in the sample (95% CI: 0 to 20%). Two males formed association bonds with their paternal brothers, no paternal brothers formed proximity bonds, and one male formed a grooming bond with his paternal brother.

Although adolescent and young adult male chimpanzees did not preferentially socialize with their paternal brothers, they did do so with their fathers. Controlling for age and age difference, adolescent and young adult male chimpanzees groomed more with their fathers than with unrelated males (Table 3.1). There was also a trend for young males to spend more time in proximity to fathers than unrelated males (Table 3.1). Since all models included kinship and age as fixed effects, the preference to socialize with fathers was present despite controlling for the age of the partner and vice versa. While males transitioning to adulthood spent considerable time grooming with their fathers, they did not preferentially associate with their fathers compared to unrelated males (Figure 3.1).

Some father-son pairs formed particularly strong bonds. Of the eleven males who had living fathers, three formed grooming bonds with them. Two males had their father as their top grooming partners. No male formed a triple bond with his father (95% CI = 0 to 10%), but one male formed proximity and grooming bonds with his father. Four of the 11 males formed at least one type of bond with their father, based on association, proximity, or grooming. In addition to the three grooming bonds displayed by father-son pairs, one male formed an association bond and another formed a proximity bond with his father.

DISCUSSION

The findings presented here indicate that adolescent male chimpanzees formed social bonds with other males. They did not differ from young adults in the number or strength of bonds that they formed. Consistent with previous research on adult male chimpanzees (Langergraber et al. 2007; Mitani 2009b; Mitani et al. 2002), adolescent and young adult male chimpanzees forged bonds with their maternal brothers and peers but not with their paternal brothers. They also forged bonds with old males, and frequently groomed with their fathers.

Given the importance of social bonds in the lives of adult male chimpanzees (Goodall 1986; Mitani 2009b; Nishida 1979), it is not surprising that they develop earlier, during adolescence. The function of social bonds among adolescents is unclear. As adults, male chimpanzees establish long-term social bonds with each other, in part, to help acquire and maintain high dominance rank (Mitani 2009a). Adolescent male chimpanzees, unlike adults, do not form decided dominance relationships with one another (Bygott 1979; Hayaki et al. 1989; Chapter 1). Adolescents therefore must be forging bonds for reasons unrelated to immediate status competition.

One possibility is that males use social bonds to buffer against the stress that they endure as adolescents. During infancy and juvenility, mothers are in near constant contact with their sons, serving as their primary grooming partner and source of support (Markham et al. 2015; Murray et al. 2014; Pusey 1983; Pusey 1990). This changes drastically during adolescence when male chimpanzees start to travel independently of their mothers. As they make this transition, adolescents receive increased aggression from adult males (Pusey 1990) and continue to remain at the periphery of parties, sometimes even after reaching adulthood (Kawanaka 1989). As a

consequence, adolescent males appear to be “less relaxed” and more “tense and inhibited” when they are around adult males (Pusey 1990: 228). Prior studies indicate that social bonds mitigate stress, as assayed by glucocorticoid levels, in female baboons (*Papio ursinus*) and adult chimpanzees (Crockford et al. 2008; Wittig et al. 2008; Wittig et al. 2016). Adolescent male chimpanzees may use social bonds in the same way, but whether they do so remains to be investigated.

A second, non-mutually exclusive possibility is that adolescent male chimpanzees forge social bonds to facilitate their entry into the social network of adult males. Immigrant female bonobos develop relationships with specific older, resident females after they immigrate into a new community (Furuichi 1989; Idani 1991). In the same way, adolescent male chimpanzees may place a premium on establishing affiliative relationships with specific adult males to expedite their integration into the network of adult male social relationships. Our findings regarding the effects of kinship and age on the formation of bonds accord with this hypothesis. Adolescent and young adult male chimpanzees appear to select their partners carefully. Maternal brothers are likely allies, as they will derive indirect fitness benefits by helping their younger siblings and have a long history of contact and familiarity due to a shared relationship with their mothers (Murray et al. 2008; Pusey 1983; Pusey 1990). Our results show that adolescent males develop association and proximity bonds with their older maternal brothers. These findings are consistent with the hypothesis that males rely on their maternal brothers as a means to enter the social network of adult male chimpanzees. Interestingly, adolescent and young adult males did not frequently groom with their maternal brothers. Although male chimpanzees may be tolerant of their younger brothers, and spend considerable time together, they do not necessarily form the more intimate bonds based on more costly behaviors such as grooming. Rather than grooming

with their adolescent younger brothers, male chimpanzees may prioritize grooming with older males who are in a position to provide coalitionary support (Watts 2002).

In addition to the bonds formed with maternal brothers, adolescent and young adult male chimpanzees developed some of their strongest social bonds with some unrelated males, who were past their prime and relatively old. Why do adolescent and young adult male chimpanzees target old males as social partners? In general, old males occupy low positions in the male dominance hierarchy and are no longer involved in the competitive world of prime adults, although they remain socially integrated (Hosaka and Huffman 2015; Nishida 2012). Adolescent and young adult males may be attracted to these “retired” males, who are more tolerant of young hangers-on than are prime adult males. The social behavior of other primates appears to change with age (Almeling et al. 2016), and across taxa, old males have sometimes been described as more relaxed than their younger selves (Dagg 2009). Few studies have investigated old age in chimpanzees (Hosaka and Huffman 2015), but one study of captive chimpanzees found that old males were less aggressive than were young adults (Baker 2000). If old males are no longer entrenched in the competitive world of adult male chimpanzees, they may make ideal partners for young males as they transition to adulthood.

In their relationships with old males, adolescent and young adult males appear to prefer certain males as social partners. In this regard, the grooming relationships between adolescent and young adult males with their fathers were unexpected and surprising, as male chimpanzees have not been shown to display paternal care (Goodall 1986). Because chimpanzees mate promiscuously, it is unlikely that they are able to discriminate paternal relatives (Langergraber et al. 2007; Wrablewski 2010). Nevertheless, two previous studies have shown that fathers interact non-randomly with their offspring. At the Tai National Park, Côte d'Ivoire, chimpanzee fathers

did not preferentially associate, groom, or play with their offspring, but when adults did play with infants or juveniles, and both offspring and unrelated youngsters were present, fathers played longer with their offspring than they did with unrelated individuals (Lehmann et al. 2006). Similarly, at Gombe National Park, Tanzania, fathers preferentially associated with the mothers of their offspring (Murray et al. 2016), a pattern that also occurs at Ngogo (Langergraber et al. 2013). In addition, infants at Gombe, while spending very little time interacting with adult males, groomed and played more often with fathers than non-relatives (Murray et al. 2016). Our observations contrast with these prior findings in an important way. Results of previous studies have been derived from observations of infants and juveniles, whose affiliative behavior is mediated, if not controlled entirely, by their mothers (Murray et al. 2014; Pusey 1983). In contrast, the relationships that we document here involve older individuals, adolescent and young adult males, who are acting independently of their mothers. The bonds that these individuals form are thus unaffected by the current social relationships of their mothers. In addition, rather than a rare but significant preference to affiliate with fathers, we found that male chimpanzees transitioning to adulthood biased their social behavior toward their fathers on a key metric of sociality, grooming.

How do the father-son grooming bonds that we have described here develop? One possibility emerges from the social, spatial, and reproductive behavior of the Ngogo chimpanzees. At Ngogo, female and male chimpanzees form social and spatial subgroups (Langergraber et al. 2009; Mitani and Amstler 2003; Wakefield 2008). Males gain a mating and reproductive advantage with subgroup females (Langergraber et al. 2013), which creates opportunities for sons to interact frequently with their fathers as they grow up. Thus, the bonds forged between

fathers and sons later in life may arise early during development via familiarity (Chapais 2008). Testing this hypothesis will require further study.

A second possibility is that adolescent and young adult males are attracted to high-ranking males (Rosenbaum et al. 2015) or formerly high-ranking males. High status is positively related to reproduction in chimpanzees; high-ranking males therefore have a stronger chance of fathering infants than do low-ranking males (Boesch et al. 2006; Feldblum et al. 2014; Gilby et al. 2013; Langergraber et al. 2013; Newton-Fisher et al. 2010; Wroblewski et al. 2009). In this study, many fathers and older males with whom adolescent and young adult males formed bonds were high-ranking in the past, creating the possibility that these relationships were forged during infancy and juvenility. Additional longitudinal study will be required to investigate the hypothesized roles of familiarity and male dominance rank on the formation of father-son bonds in chimpanzees.

Taken together, our findings reveal that adolescent male chimpanzees form social bonds with other males and that the bonds forged between adolescents and their maternal brothers, old males, and fathers may play an important role during the transition to adulthood. If bonds between fathers and adolescent or adult sons exist in chimpanzee more generally, it offers insight into how pair bonding in humans, featuring relatively exclusive mating and extensive paternal care, could have evolved from phylogenetic building blocks already present in a more promiscuous chimpanzee-like social and mating system. Understanding the demographic, socioecological, and other factors that lead to father-offspring bonds in chimpanzees is likely to furnish novel insights into transitions in the nature of the father-offspring relationship that occurred during hominin evolution (Chapais 2008).

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Figure 3.1. Social bonds formed by adolescent and young adult male chimpanzees. Values for dyadic (a) association frequencies, (b) proximity frequencies, and (c) grooming rates are shown. Orange points are dyadic values in the top 10% of the distributions involving young adults and adults. Grey points are dyadic values in the lower 90% of the distributions.

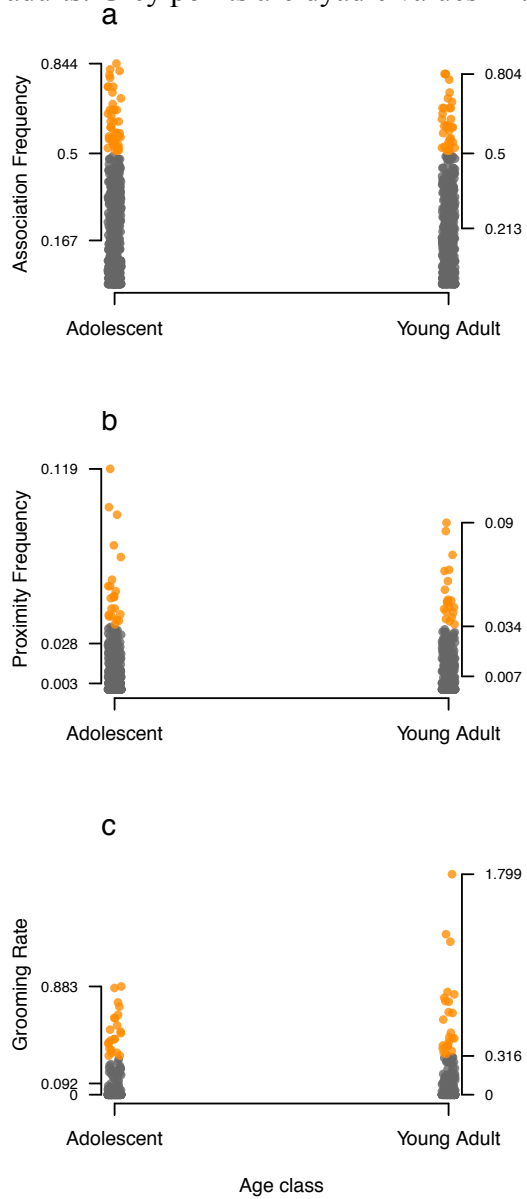


Table 3.1. Models of association, proximity, and grooming between adolescent/young adult males and other males predicted by kinship, age of the subject, age of the partner, and age difference of the pair. The variables in bold typeface represent significant predictors ($P < 0.05$).

Variable statistics							
Outcome	Fixed effects	β	SE	z value	P value	Random effects	Variance
Association	Focal Age	0.001	0.013	0.040	0.968	Subject	4e-07
	Maternal Brother	0.874	0.238	3.675	0.0002	Partner	0.396
	Paternal Brother	-0.021	0.168	-0.125	0.900		
	Father	0.173	0.291	0.593	0.553		
	Partner Age	0.024	0.009	2.819	0.005		
	Age Difference	-0.008	0.011	-0.852	0.394		
	log(Following episodes)	0.991	0.505	1.963	0.050		
Proximity	Focal Age	-0.003	0.030	-0.108	0.914	Subject	0.253
	Maternal Brother	0.936	0.235	3.982	7e-05	Partner	0.238
	Paternal Brother	0.204	0.216	0.944	0.345		
	Father	0.580	0.296	1.956	0.051		
	Partner Age	0.051	0.010	5.328	9e-08		
	Age Difference	-0.038	0.012	-3.247	0.001		
	log(Association)	1.454	0.067	21.582	< 2e-16		
Grooming	Focal Age	0.123	0.080	1.615	0.106	Subject	0.694
	Maternal Brother	0.180	0.712	0.253	0.80	Partner	0.676
	Paternal Brother	-0.992	0.651	-1.523	0.128		
	Father	2.054	0.808	2.543	0.011		
	Partner Age	0.108	0.025	4.293	2e-05		
	Age Difference	-0.067	0.031	-2.183	0.029		
	log(Association)	1.832	0.174	10.532	< 2e-16		

Figure 3.2. Number of social bonds formed by adolescent and young adult male chimpanzees. The number of association, proximity, and grooming bonds formed by each male is shown. Values are ordered on the x-axis by age of the individual male, increasing from left to right.

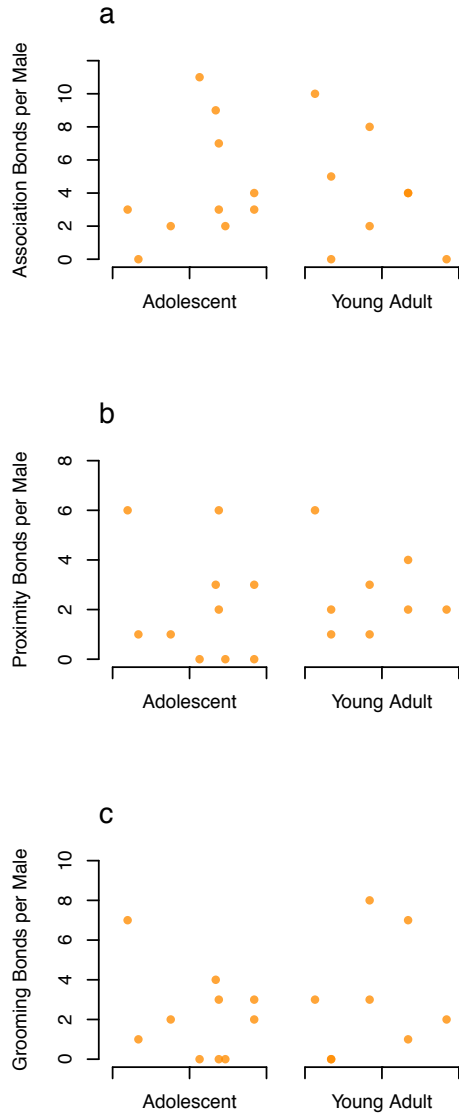
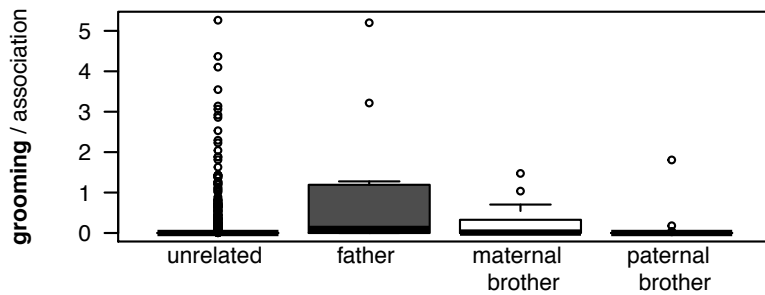
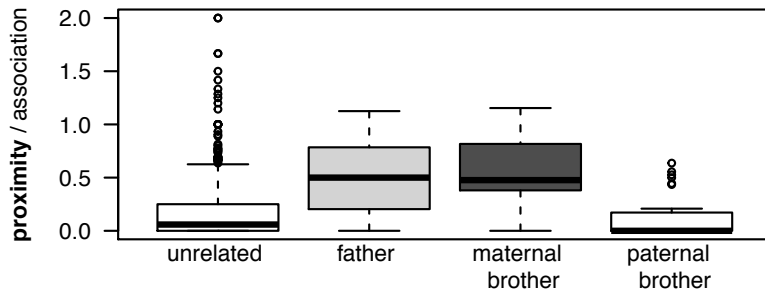
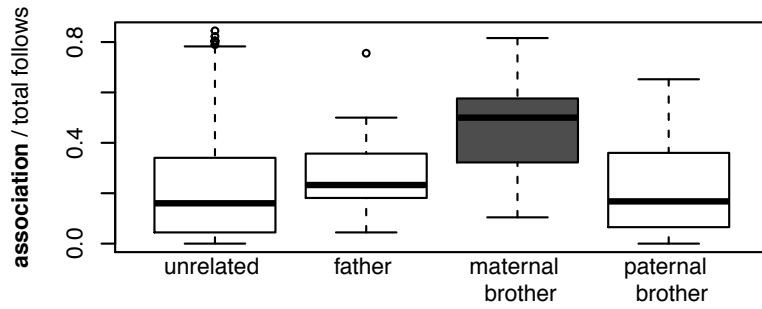


Figure 3.3. Social bonding and kinship. (a) Association relative to total observation time. (b) Proximity relative to total association time. (c) Grooming relative to total association time. Boxplots are shown for illustrative purposes only. Statistical tests were conducted using multiple regression of relatedness, age, and age difference (Table 3.1).



CHAPTER 4

Familiarity and male dominance rank influence father-son social relationships in wild chimpanzees

ABSTRACT

In mammals, father-offspring bonds occur primarily in monogamous species, where paternity is certain and fathers care for offspring. Nevertheless, some primates, who mate promiscuously, display father-offspring relationships. Behavioral mechanisms, such as familiarity mediated by the mother and dominance rank of the father, may explain such relationships. Recently, we documented novel father-son bonds in a promiscuously-breeding primate: adolescent and young adult male chimpanzees (*Pan troglodytes*) form strong grooming bonds with their fathers at Ngogo in Kibale National Park, Uganda. How do chimpanzee sons single-out their fathers as grooming partners? Here we find that father-son bonds are due, in part, to relationships formed when adolescent and young adults were infants and juveniles. Adolescent and young adult males groomed formerly high-ranking males and joined subgroups with older males who ranged in the same part of the territory as their mothers did in the past. Thus, as males transition to adulthood they form bonds with old, formerly high-ranking males with whom they are familiar. Until recently, father-son bonds were considered evolutionarily derived in humans. Our results force a reevaluation of current models of the evolution of human fatherhood and raise the possibility that “fatherhood” was first initiated not by fathers, but instead by sons.

INTRODUCTION

Kinship affects the social lives of mammals (Sherman 1977; Smith 2014). Mothers care for their infants, and, in some species, mothers form lifelong bonds with their offspring. This is the case in many primates. Bonds with mothers as well as maternal siblings, aunts, and nieces, define the social world of many female monkeys (Chapais 2001; Gouzoules 1984; Silk 2007; Silk 2002). Maternal kinship also plays an important role in some male primates. For example, adult male chimpanzees (*Pan troglodytes*) form strong cooperative relationships with their maternal half-brothers (Langergraber et al. 2007; Mitani 2009). A bias toward maternal kin is likely to develop due to shared familiarity with the mother (Chapais 2001; Gouzoules 1984; Rendall 2004).

Although social relationships between maternal kin are common in primates, kin selection should also promote bonds between paternal relatives (Berman 2015). Doing so, however, may be difficult for primates who live in multi-male, multi-female groups, mate promiscuously, and do not exhibit paternal care (Gouzoules 1984; Strier 2004). In these situations, single females mate multiple males, and paternity is often uncertain. There is therefore no reason to suspect that paternal kin, be it fathers and sons or paternal half-siblings, can identify each other.

Despite these considerations, some primates have been found to bias their social behavior toward paternal relatives. In macaques (*Macaca mulatta*), baboons (*Papio ursinus*, *P. cynocephalus*), and mandrills (*Mandrillus sphinx*), infants and juveniles spend time in spatial proximity to specific adult males who are often their fathers (Berenstain et al. 1981; Charpentier et al. 2007; Huchard et al. 2010; Huchard et al. 2013; Langos et al. 2013; Ostner et al. 2013), and

fathers intervene on behalf of their infant and juvenile offspring in aggressive encounters (*P. cynocephalus*: Buchan et al. 2003). Paternal siblings also favor one another over unrelated pairs in several primate species (Schülke et al. 2013; Smith et al. 2003; Widdig et al. 2016; Widdig et al. 2001).

How do group-living primates recognize paternal kin? Even in promiscuously mating species, paternal kin may become familiar with each other due to a shared bond with the mother, a general overlap in space and time, and other social cues correlated with paternity, such as rank (Busse 1985; Rendall 2004; Smith et al. 2003; Widdig 2007). In some baboon species, adult females form strong social bonds with adult males, and these pairs often mate (e.g. *Papio ursinus*, Smuts 1985). The infants of these females grow up in close proximity to their mother's adult male "friend," they tend to develop a relationship with that adult male, and the male friend is often, but not always, their father (Huchard et al. 2010; Huchard et al. 2013; Moscovice et al. 2009; Palombit et al. 1997). Similar situations occur in primate species where males and females do not exhibit strong bonds. Maternal familiarity and co-residence patterns predict adult male - infant bonds, even when the adult male is not the father (Berenstain et al. 1981; Kerhoas et al. 2016; Langos et al. 2013).

In addition to familiarity due to maternal behavior, male dominance rank may influence the behavior of paternal kin. High-ranking male primates typically father more offspring than do low-ranking males (Alberts 2012). As a result, high-ranking males may invest more in parental effort or, due to demographic factors, may encounter their own offspring more often than unrelated infants (Busse 1985; Pope 1990). In capuchin monkeys (*Cebus capucinus*) and gorillas (*Gorilla beringei*), dominance rank influences relationships between adult males and infants and

juveniles, including bonds between fathers and offspring (Rosenbaum et al. 2015; Sargeant et al. 2016).

Recently, we have documented novel father – son social bonds in a promiscuously breeding primate. Adolescent and young adult male chimpanzees form strong grooming bonds with their fathers at Ngogo in Kibale National Park, Uganda (Chapter 2). These bonds are unexpected given the promiscuous mating system of chimpanzees (Goodall 1986; Mitani et al. 2000; Tutin 1979). Previous studies of male chimpanzees at Ngogo indicate that maternal half-brothers form strong social bonds with each other, but paternal half-brothers do not (Langergraber et al. 2007; Mitani 2009; Mitani et al. 2002). In addition, a study at Gombe National Park, Tanzania, found that fathers do not bias their social behavior toward their juvenile or adolescent sons (Wroblewski 2010). In contrast, two other studies have demonstrated paternal kin biases in chimpanzees. Adult male chimpanzees at Gombe played more often with their own infant offspring than expected by chance (Murray et al. 2016). Additional research at Tai National Park, Côte d'Ivoire, found that adult male chimpanzees played with their infant and juvenile offspring for longer periods than they did with unrelated young (Lehmann et al. 2006). While these reports of father -offspring relationships in chimpanzees are intriguing, they lack a clear mechanism. As a consequence, paternal biases in behavior could represent false positives reflecting Type I statistical error (Gouzoules 1984; Silk 2002), as was the case in earlier studies reporting paternal kin relationships in macaques (*Macaca nemestrina*) (Wu et al. 1980).

Prior research at Ngogo identifies two potential behavioral mechanisms for how fathers might familiarize themselves with their sons: via male-female co-residence patterns and male dominance rank. Sons may grow up encountering their fathers more than other males (Langergraber et al. 2013). Chimpanzees live in fission-fusion communities in which individuals

form temporary subgroups or parties throughout the day (Goodall 1986; Nishida 1979). Adult females occupy relatively small core areas within the larger communal territory (Emery Thompson et al. 2007; Murray et al. 2007; Wakefield 2008; Williams et al. 2002). Adult males tend to travel throughout their entire territory, but they too form cliques and frequent certain areas within their range (Mitani and Amstler 2003; Murray et al. 2008). At Ngogo, males and females who associate frequently and range over similar parts of the territory are more likely to reproduce together (Langergraber et al. 2013). This increases the probability of adult males occupying similar parts of the territory as their offspring, thereby providing an opportunity to become familiar with those individuals (Langergraber et al. 2013). During the transition to adulthood, male chimpanzees may seek and associate with older males with whom they are familiar from their time growing up (Nishida 2012; Pusey 1990).

In chimpanzees, male dominance status affects reproduction; high-ranking males father more infants than do lower-ranking individuals (Boesch et al. 2006; Feldblum et al. 2014; Gilby et al. 2013; Langergraber et al. 2013; Newton-Fisher et al. 2010; Wroblewski et al. 2009). Old, formerly high-ranking males are therefore likely to be the fathers of adolescent and young adult males. Adolescent and young adult males, in turn, may be attracted to these same males who were high-ranking in the past. Infant and juvenile gorillas maintain proximity to high-ranking males (Rosenbaum et al. 2015), and similar preferences for high-ranking adult males patterns may occur in immature chimpanzees (Pusey 1990).

Here, we investigate whether past co-residence patterns and past male rank predict current association, proximity, and grooming behavior of males transitioning to adulthood. We compared the current social relationships of these males with observations of the spatial and social behavior of their mothers eleven years previously (Langergraber et al. 2013; Langergraber

et al. 2009). These data furnish a snapshot into the lives of adolescent and young adult males when they were infants and juveniles.

METHODS

Study site and subjects

We conducted observations of chimpanzees at Ngogo, Kibale National Park, Uganda, over 12 months from August 2014 through August 2015. During the study period, the Ngogo chimpanzee community consisted of 193 individuals, including 23 adolescent males (8-16 years) and 31 adult males (17-53 years). Subjects were 18 adolescent and young adult male chimpanzees between 12 and 21 years old.

Detailed observations of adult females, who are the mothers of our subjects, were initiated in 2003. Thus, most of our adolescent and young adult male subjects were identified as infants and juveniles, and their birth dates are known to within 1 month to 1 year. Because continuous study of chimpanzees at Ngogo began in 1995, the exact ages of many adults are unknown. Their ages have been estimated based on their physical appearance, behavior, and genetically established pedigrees (Wood et al. 2017).

Genetic relationships between all of our subjects are known based on prior behavioral observations and genetic analyses of autosomal, X-chromosomal, and Y-chromosomal microsatellite loci, and of mitochondrial DNA (Langergraber et al. 2007; Langergraber et al. 2013; Langergraber et al. 2009). Male pairs were assigned as fathers and sons, maternal half-siblings, paternal half-siblings, or unrelated. The last category comprised dyads not assigned to the first three groups and included distant relatives such as uncles and nephews and first cousins.

Eleven adolescent and young adult males had fathers, who were alive at the time of this study; they included six males.

Behavioral observations

A.A.S. conducted behavioral observations of adolescent and young adult males during focal sampling sessions lasting one hour (mean \pm SD hours of observation per subject = 43 ± 3.2 hours, $N = 18$ males). While following focal males, he collected data on three components of chimpanzee social relationships: association, proximity, and grooming (Chapter 3). Given the fission-fusion nature of chimpanzee society, males associate with only a subset of individuals in their community at any given time (Goodall 1986; Nishida 1979). They do so in temporary subgroups or parties that change in size and composition. Males who traveled together or encountered one another during hour-long following episodes were scored as being in party association with focal subjects. Individuals in proximity (< 5 meters) to the focal subject were recorded during instantaneous point samples made at 10-minute intervals. All occurrences of grooming between the focal subject and other individuals were recorded to the nearest second.

Observations of female and male subgroup associations and space use were recorded eleven years before this study in 2003 and 2004 by K.E.L. (Langergraber et al. 2013; Langergraber et al. 2009). These observations represent the past behavior of current adolescent and young adult males when they were dependent on their mother as infants and juveniles. Because infant and juvenile chimpanzees are in near constant contact with their mothers (Pusey 1983), maternal subgroup associations and space use are likely to reflect those of their infant and juvenile sons. Instantaneous point samples were conducted at half hour intervals to record adolescent and adult individuals in association with focal female subjects and their locations in the territory.

To assess the past dominance status of old males, we used data on pant grunts, a formal signal of submission directed up the hierarchy and given by low-ranking chimpanzees to higher-ranking individuals (Bygott 1979; De Waal 1982). Observations of male pant grunts exchanged between males were recorded by J.C.M. from June to August in 2003 and 2004.

Statistical Analyses

The past association and residence patterns of mothers of our adolescent and young adult subjects provide an indication of who their sons are likely to have encountered frequently in youth. These data can be used to evaluate whether familiarity influences current social relationships. We computed pairwise affinity indices between mothers and male chimpanzees to determine maternal association patterns in 2003 and 2004. Numerically this index is:

$$\frac{I_{ab} * \sum s_i(s_i - 1)}{\sum a_i(s_i - 1) * \sum b_i(s_i - 1)}$$

where I_{ab} = the number of appearances of a and b together, a_i = the number of appearances of a, b_i = the number of appearances of b, s_i = the size of group i (Pepper et al. 1999). Observed indices were normalized by dividing them by their expected values generated by a randomization procedure (Langergraber et al. 2013; Pepper et al. 1999). Expected values were produced to reflect a situation where mothers associated with others randomly.

To assess similarity in space use between mothers and male chimpanzees in 2003 and 2004, a map of 500 x 500 m grid cells were overlaid the Ngogo chimpanzee community territory. We then summed how often each individual used each 500 x 500 m grid cell, and calculated Spearman rank correlation coefficients of grid cell use frequency (Doncaster 1990). This “Doncaster Index” varies from 1 when the ranks of grid cell use frequency for two individuals

are identical to -1 when the two individuals never use the same grid cell. Doncaster indices of space use similarity and pairwise affinity indices of association are strongly but not perfectly positively correlated between male-female pairs (Pearson's correlation = 0.691, 95% confidence interval = 0.613 – 0.756), as individuals can use the same areas of the territory but at different times.

We also assessed the influence of the prime- and old males' past rank on current social relationships. To determine the past rank of older adult males, we combined pant grunts exchanged between males in 2003 and 2004 into a single giver-receiver matrix. We calculated David's scores using DomiCalc (Schmid and de Vries 2013), and z-transformed the David's score for use in statistical analyses (Schielzeth 2010).

In the following, we restrict analyses to old adult males who had reached adolescence in 2003 (mean age = 22.5 years, range = 11- 42 years) and were thus potential social and reproductive partners for the mothers of our subjects. We constructed three sets of generalized linear mixed models (GLMMs) with association, proximity, and grooming between adolescent and young adult male subjects and older adult males in 2014-2015 as the outcome variables. Predictor variables included: 1) association between the older male and the male subjects' mother in 2003-2004 ("past associations"); 2) space use similarity between the older male and the younger male's mother in 2003-2004 ("past space use"); 3) the older male's dominance rank in 2003-2004 ("past rank"); and 4) whether the older male was the younger male's father. All fixed effects were centered and z-transformed to make them more easily interpretable given that some models included interaction terms (Schielzeth 2010). The identities of subjects and partners were included as random effects. For the association models, we included the logarithmically-transformed number of observation hours as a fixed effect to control for variation in the number

of times we followed each male in 2014-2015. For the proximity and association models, we included the logarithmically-transformed number of following episodes dyads were in association in 2014-2015 as a fixed effect to control for opportunities of males to interact. We set a negative binomial error distribution for each model.

We constructed 16 models that included various combinations of the fixed effects and ranked them using Akaike's Information Criteria (AIC) (Burnham and Anderson 2002). We considered the model with lowest AIC value to be the best approximating model (Burnham et al. 2011; Richards et al. 2011). Models with a change in AIC values > 3 from the best approximating model were considered to have weak support, and we rejected models with a change in AIC values > 10 as these were unlikely to furnish a high degree of explanatory power. We considered variables that appeared in all of the top models to be influential predictors and present averaged coefficients from all models (Richards et al. 2011).

RESULTS

Past behavior predicted current social relationships between males transitioning to adulthood and older adult males. Past space use and the rank of the older male at the time were good predictors of current associations displayed by adolescent and young adult males (Figure 4.1). These two variables appeared in four of the five best models (Table 4.1). The second best model explaining current association patterns included past space use and past rank of the older male (Δ AIC = 0.66), while the third best model included past space use, past rank, and an interaction between the two (Δ AIC = 1.05). The interaction was negative, indicating that as past rank of the older male increased or decreased, the effect of past space use decreased and

increased, respectively. All models with past space use or past associations performed considerably better than the null model ($\Delta AIC = 41.3$) or the model with observation effort alone ($\Delta AIC = 42.63$).

Paternity consistently appeared as a predictor of current grooming in all of the six top models (Table 4.1c). This finding replicates results of our previous analyses that documented strong grooming bonds between fathers and sons (Chapter 3). The past dominance rank of older males and past maternal space use and associations, however, also had effects on the grooming behavior of adolescent and young adult male chimpanzees. The past dominance rank of older adult males appeared in five of the six top models produced via the GLMM analyses (Table 4.1c). Controlling for paternity, past maternal space use or past associations also appeared in some of the top models; they did so twice and once, respectively (Table 4.1c).

Few variables emerged as strong predictors of current proximity relationships (Table 4.1b). The past rank of older males appeared as a predictor of current proximity relationships, but it did not considerably improve the model compared to the one with current association alone ($\Delta AIC = 0.65$). This suggests that there are other factors mediating spatial proximity unaccounted for in these analyses.

DISCUSSION

During adolescence, male chimpanzees form social bonds with other males in their community (Chapter 3). Some of the strongest grooming bonds occur between adolescents and old adult males, including their fathers (Chapter 3). Results of the analyses presented here

suggest that familiarity and male dominance rank mediate these unexpected bonds between chimpanzee fathers and sons.

We found that past co-residence patterns between males and adult females predicted current party associations between these males and the male offspring of those females and who are now adolescents and young adults. Specifically, adolescent and young adult males associate with old males who had selectively used similar parts of the territory as their mothers in the past when the adolescents and young adult males were infants and juveniles (Figure 4.1a). In addition, paternity appears to influence the grooming relationships of adolescent and young adult male chimpanzees, as these males groom frequently with their fathers (Figure 4.2). Male dominance rank, along with familiarity as assayed by past maternal space use and associations, appear to mediate these interactions. Adolescent and young adult male chimpanzees groom with old adult males who were formerly high ranking and with whom their mothers associated in the past when they were infants and juveniles.

Since rank is positively related to reproduction in chimpanzees, males who were high-ranking in the past are likely to be the fathers of adolescent and young adult male. As a consequence, and because male chimpanzees are philopatric, grooming relationships may develop between fathers and sons as a byproduct of the effect of rank on reproduction (Boesch et al. 2006; Langergraber et al. 2013; Newton-Fisher et al. 2010; Wroblewski et al. 2009). In other primates, father-offspring relationships develop as a result of alpha males monopolizing mating opportunities (Pope 1990; Rosenbaum et al. 2015). The striking aspect about the findings presented here is that male chimpanzees form relationships with their fathers twelve to twenty years after conception. High rank may be a good cue of paternity during infancy (Borries et al. 1999), but adolescent and young adults groomed with old males who were high-ranking many

years earlier. This raises the intriguing possibility that adolescent and young adult males remember the past rank of adult males, and use this to choose grooming partners.

Previous familiarity and previous rank influence the current bonds between fathers and sons. In this regard, the father-offspring relationships that occur in chimpanzees are similar to those found in other promiscuously mating primates. In baboons (*Papio ursinus*, *P. cynocephalus*), mothers appear to broker the bonds between fathers and sons, as females often form strong relationships with their mates (Huchard et al. 2010; Huchard et al. 2013; Moscovice et al. 2009; Palombit et al. 1997). While strong social bonds between males and females are not a salient part of chimpanzee behavior (Goodall 1986; Lehmann et al. 2006; Machanda et al. 2013), associations between them influence reproduction (Langergraber et al. 2013). This familiarity brought about through such maternal association may be sufficient to impact their sons' social decisions later in life. Male dominance rank also affects social relationships between adult males and immature individuals in other primates and provides a mechanism for the bonds formed between fathers and offspring (Godoy et al. 2016; Rosenbaum et al. 2015). While the grooming relationships between fathers and sons in chimpanzees are unexpected, we have provided a plausible mechanism for how they develop. In doing so, this study adds to the growing body of literature on paternal relationships in primates in the absence of monogamy.

There are several limitations of this study. First, we used data on past maternal behavior from only one year when adolescent and young adult males were infants and juveniles. Observations across their entire period of development would provide a more accurate way to evaluate the effect of familiarity on father-son relationships. Second, additional behaviors apart from maternal associations and space use and male rank, such as grooming behavior and spatial proximity, might yield insights into how past relationships influence current behavior. Third, we

have not investigated past relationships between infants and juveniles and adult males. Space use and associations between mothers and adult males served as proxies and do not specifically indicate what actually occurs between the infants and juveniles and adult males. At Gombe National Park, Tanzania, adult male chimpanzees play frequently with their infant offspring, an effect prominent only in the first 6 months of their infants' lives (Murray et al. 2016). Our preliminary data indicate that infants, juveniles, and early adolescents occasionally play with adult males (n = 159 bouts), including fathers (n = 7 bouts; 5 father-son dyads). The role of play in forming bonds with adults, including fathers, remains to be explored.

Our results provide support for a model for the evolution of father-offspring relationships in humans (Chapais 2008). Chapais (2008) hypothesized that father-son bonds may have arisen in our human ancestors from a chimpanzee-like social system. Building on preliminary findings that adolescent male chimpanzees socialize with old males (Kawanaka 1989), Chapais proposed that bonds with fathers could develop if males and females formed social relationships with each other. Our finding that past male-female space use predicts current male-male associations is consistent with this hypothesis. According to Chapais (2008, p. 195): "The idea that father-child recognition unfolds not so much from paternal care but from the father's long-term association with the mother bears upon one well-recognized anthropological fact. In the vast number of human societies, legal fatherhood is determined on the basis of the mother-husband association." Studies indicate that from ancient Rome, to the Nuer of Sudan, and more recently in Norway, the husband of the mother was considered the legal father, regardless of genetic paternity (Holy 1996).

In this and several other ways, father-son relationships between chimpanzees are similar to those displayed by humans. In some human populations, fathers provide little or no care to their

infants (Sear and Mace 2008), but instead support them later in life (Hewlett and MacFarlan 2010; Scelza et al. 2010). Humans take a long time to grow up, and social relationships are particularly important during adolescence (van Harmelen et al. 2016; Yang et al. 2016) when adolescents form intimate bonds with peers and adults outside of the family (Berndt 1992). Many adolescents in industrial societies forge strong bonds with adults, who are not their parents, and these mentors improve the emotional and psychological well being of adolescents (Beam et al. 2002; Greenberger et al. 1998; Lourenco et al. 2015). Similar patterns are found in some foraging societies, for example, in the Martu of Australia, where fathers expedite initiation of boys into the social hierarchy of adults, which leads to their ability to reproduce (Scelza et al. 2010). Thus, fathers and father figures play important roles in the lives of young males during the transition to adulthood, and these relationships have health, emotional, and reproductive benefits (Scelza et al. 2010; Sheppard and Sear 2011). It remains to be investigated whether the father-son bonds in chimpanzees benefits young males. Given the importance of social bonds in adulthood, young males may have fitness benefits if bonds with old adult males and fathers expedite their entrance into the adult social network.

Until recently, father-offspring bonds were thought to be absent in our closest living relatives, and were considered evolutionarily derived, developing after the split between humans and chimpanzees (Chapais 2008; Gray and Anderson 2010). Our findings force a reevaluation of this hypothesis, as father-son relationships may have emerged in a chimpanzee-like social system and may have preceded the evolution of pair bonds. If this is the case, it also raises the possibility that “fatherhood” may have been first initiated not by fathers, but instead by sons.

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Table 4.1. Influence of past maternal behavior, past male rank, and paternity on current affiliation patterns of adolescent/young adult males with prime and old adult males. Top models ($\Delta AIC < 3$ or models with lower AIC than the model with only current association) presented below. We constructed 16 total models, with combinations of potentially informative predictors. Models that included both past maternal space use and association were excluded as the two are highly correlated. Averaged coefficients across the full set of models are included below top models.

A. Current Association													
Model	Father	Past Rank	Past Space	Past Assoc	Father: Past Space	Father: Past Rank	Past Space: Past Rank	Father: Past Assoc	Past Assoc: Past Rank	Total Follow	Intercept	Δ AIC	Weight
1			0.743							0.317	2.345	0	0.29
2		0.120	0.742							0.314	2.345	0.66	0.21
3		0.126	0.717				-0.102			0.301	2.346	1.05	0.17
4		0.107		0.679					-0.199	0.232	2.347	2.41	0.09
5	0.016	0.118	0.741							0.314	2.344	2.63	0.08
Avg	-0.001	0.077	0.572	0.161	0.008	0.001	-0.017	0.001	-0.017	0.298	2.344		

B. Current Proximity													
Model	Father	Past Rank	Past Space	Past Assoc	Father: Past Space	Father: Past Rank	Past Space: Past Rank	Father: Past Assoc	Past Assoc: Past Rank	Current Assoc	Intercept	Δ AIC	Weight
1		0.097								2.735	0.778	0	0.15
2										2.762	0.782	0.65	0.11
Avg	0.053	0.061	0.001	-0.049	-0.004	-0.003	-0.013	-0.006	0.002	2.772	0.777		

C. Current Grooming													
Model	Father	Past Rank	Past Space	Past Assoc	Father: Past Space	Father: Past Rank	Past Space: Past Rank	Father: Past Assoc	Past Assoc: Past Rank	Current Assoc	Intercept	Δ AIC	Weight
1	0.806									2.596	0.445	0	0.32
2	0.732	0.149								2.575	0.420	1	0.19
3	0.792	0.158	0.403							2.451	0.401	2.34	0.1
4	0.730	0.134		-0.319						2.740	0.422	2.54	0.09
5	0.767	0.170	0.452		-1.280	-0.135				2.630	0.356	2.6	0.09
6	0.904	0.153				-0.140				2.612	0.432	2.68	0.08
Avg	0.702	0.113	0.083	-0.042	-0.112	-0.026	-0.025	-0.004	-0.003	2.569	0.427		

Figure 4.1. Association patterns of adolescent and young adult males with older adult males. Current association is influenced by past space use. Figure is for illustrative purposes only. Statistical tests were done using multiple multivariate, generalized linear mixed models and ranked with AIC (Table 4.1). Blue points indicate father-son pairs (N = 11).

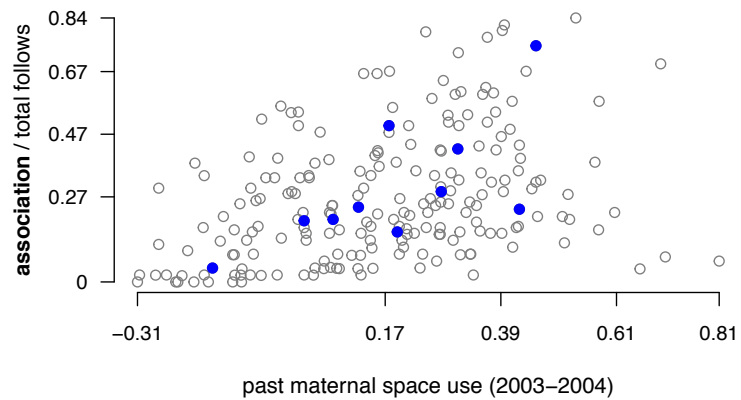
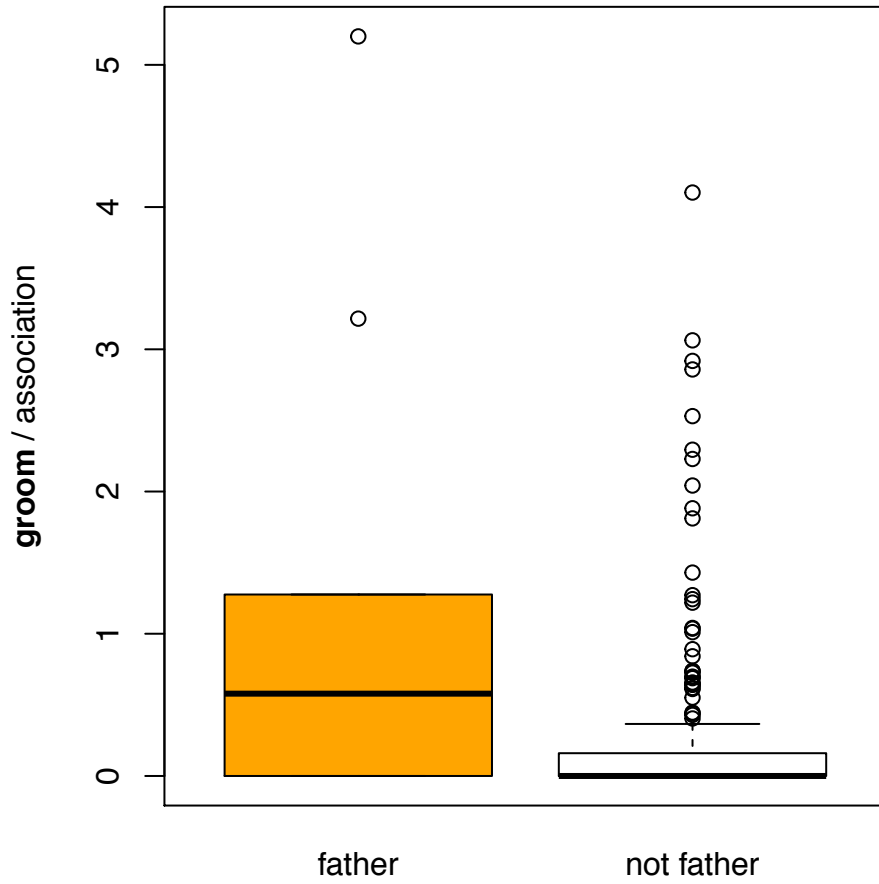


Figure 4.2. Grooming with fathers and other older adult males. Paternity predicts grooming between males transitioning to adulthood and older adult males. Statistical tests were done using multiple multivariate, generalized linear mixed models and ranked with AIC (Table 4.1).



CHAPTER 5

Conclusion

Adolescence is a distinct social phase in male chimpanzees (*Pan troglodytes*). Until now, very little was known about this period of development (Hayaki 1985; Hayaki et al. 1989; Kawanaka 1989; Kawanaka 1993; Pusey 1990). Adult male chimpanzee life is centered on jockeying for dominance rank and maintaining social bonds. Do these relationships emerge during adolescence? Based on research at Ngogo in Kibale National Park, Uganda, this dissertation produced four main findings. First, adolescent male chimpanzees *do not* form a dominance hierarchy with other adolescents. Second, adolescent male chimpanzees *do* form social bonds with other males. Third, these social bonds are formed with maternal brothers, peers, old males, and, surprisingly, fathers. Fourth, bonds with old males and fathers are explained by the past space use and rank of older males when adolescent and young adult male chimpanzees were infants and juveniles.

Delaying dominance, making friends

Adult male chimpanzees seem to eat, live, and breathe to compete and to establish their dominance over others (Bygott 1979; De Waal 1982). I have shown that adolescent male chimpanzees, in stark contrast to adults, do not compete for status with their peers. This surprising finding leads to an obvious question: Why wait? One possibility is that adolescent

male chimpanzees are preoccupied with dominating females, and it is only at the end of adolescence after this is accomplished that they can turn their attention to competing with their male peers. Alternatively, adolescent male chimpanzees may forego aggressive encounters with other males to appear less threatening to adult males, thereby reducing potential aggression from them. Since adolescent male chimpanzees must integrate into the social world of adult males, characterized by both cooperation and competition, adolescent males prioritize affiliative relationships over agonistic interactions. The results presented in this dissertation are consistent with this suggestion.

In Chapter 2, I found that adolescent male chimpanzees form social bonds with other males. Given the importance of social bonds in adulthood, it is not surprising that bonds arise during adolescence, as had been suggested by previous studies (Kawanaka 1989; Kawanaka 1993; Pusey 1990). Both adolescent and young adult male chimpanzees form social bonds with peers and maternal brothers. This is similar to patterns displayed by older adult males (Langergraber et al. 2007; Mitani 2009). Adolescents and young adults, however, forge some of their strongest bonds with relatively old adult males. In the same way that adolescents avoid dominance interactions, male chimpanzees transitioning to adulthood appear to seek out old males who are no longer entrenched in the competitive world of adults. These old males, having entered a form of “retirement,” are typically tolerant of younger males. In a further twist to this story, some of the old males with whom adolescent and young adult males form friendships are their fathers.

The social bonds that I have documented between adolescent and young adult males with their fathers are unexpected. Bonds between males transitioning to adulthood and fathers have not been demonstrated before in chimpanzees (Wroblewski 2010). Because chimpanzees mate promiscuously (Tutin 1979), there is no reason to suspect that young male chimpanzees can

recognize their fathers or that fathers can recognize their sons. Yet adolescent and young adults at Ngogo seek out their fathers. They spend considerable time grooming old males, especially their fathers. Fathers, on the other hand, almost never groom adolescent or young adult sons. In general, older adult males do not maintain close spatial proximity or bias their grooming behavior toward their sons. Thus, the bond is largely from the sons' perspective rather than the fathers. How do chimpanzees "find" their fathers?

Recognizing paternal kin

I identified a mechanism that might lead sons to form social bonds with their fathers. At Ngogo, both female and male chimpanzees partition the communal territory, showing distinct preferences to range in certain neighborhoods or socialize within certain cliques (Langergraber et al. 2009; Mitani and Amstler 2003; Pepper et al. 1999; Wakefield 2008). Males gain a mating advantage with neighborhood females and are likely to reproduce with them (Langergraber et al. 2013). Offspring produced from such unions remain in their mother's neighborhood as they grow up, so it is likely that they become familiar with their fathers. In Chapter 3, I showed that adolescent and young adult male chimpanzees join subgroups with older males who had occupied their mother's neighborhood in the past. Thus, adolescent and young adults associate with males with whom they are familiar from infancy and juvenility. Some of these older males are coincidentally their fathers. In addition, adolescent and young adult males tend to groom formerly high-ranking males. Old, formerly high-ranking males are more likely to have adolescent and young adult offspring because of the positive relationship between rank and reproduction. Past rank of the older male, however, does not completely explain the bias toward grooming with fathers.

It is possible that chimpanzees possess an ability to recognize paternal kin. Other mammals use their own phenotype as a referent to compare to others through a process known as “phenotype matching” (Holmes and Sherman 1982; Holmes and Sherman 1983; Mateo and Johnston 2000). Some species use olfactory cues. Dubbed the “armpit effect,” an animal might smell itself and match its odor to that of kin (Dawkins 1982). Can chimpanzees use olfactory cues to recognize kin, as is the case in rodents (Heth et al. 1998; Mateo and Johnston 2000)? This seems unlikely, given the relative reduction in olfaction in catarrhines (Smith et al. 2007). Nevertheless, the olfactory abilities of primates, including chimpanzees are likely underestimated (Drea 2015). Chimpanzees sniff the ground on patrols of their border and within their territory, and they sniff the estrous swellings of female chimpanzees (Goodall 1986; Matsumoto-Oda et al. 2007; Nishida 1997; Wallis and Lemmon 1986). In addition, chimpanzees, along with gorillas and humans, exhibit an aggregation of apocrine glands in the axillary region (Ellis and Montagna 1962; Montagna 1972; Montagna and Yun 1963). Could the pungent odor from the great ape armpit be a way of identifying kin? It is also possible that chimpanzees distinguish kin through facial features. Human researchers at Ngogo often see striking similarities between both maternal and paternal kin (Figure 1), and there is experimental evidence suggesting that humans as well as captive chimpanzees may be able to do this (Parr et al. 2010). Unlike smelling an armpit, however, there is no obvious way that a chimpanzee knows what he himself looks like. Further study is needed to investigate the abilities of chimpanzees to recognize kin.

Beyond this study

Future work should seek to replicate my finding that adolescent and young adult chimpanzees form bonds with their fathers. It remains unclear whether the bias is limited to

Ngogo or is present at other sites. With the large size and long lives of males at Ngogo (Wood et al. 2017), it is possible that fathers and sons are likely to encounter one another, especially given the mating and social patterns there (Langergraber et al. 2013). Despite this, father-offspring relationships are not unique to Ngogo.

Paternal relationships appear to play an important role in chimpanzee behavior than previously thought. Although the past behaviors I investigated did not fully explain the grooming bonds between teenage sons and their fathers, other past behaviors may do so. Evidence from other sites suggests that chimpanzee fathers play more often or for longer durations with their offspring than expected (Lehmann et al. 2006; Murray et al. 2016). If it is true that infant chimpanzees have special relationships with fathers, those behaviors could translate into grooming bonds later, when adolescent and young adults are independent of their mother and integrating into the social network of adult males.

If a bias toward paternal kin is prevalent in chimpanzees, it encourages us to question assumptions about kin recognition and the nature of social bonds. What are the mechanisms that drive social bonds in chimpanzees and other primates, including humans? To understand the role of kinship on social bonds in chimpanzees, it is important to investigate the ontogeny of these relationships. In Chapter 2, I found that by middle and late adolescence, male chimpanzees form bonds similar to those of young adults. But the social relationships of adolescents and young adults may differ from those of prime- and old adults (Kawanaka 1993). In addition, bonds may develop even earlier. Infants and juveniles spend considerable time playing with others (Hayaki 1985; Lonsdorf et al. 2014; Murray et al. 2014). Do infants, juveniles, and early adolescents prefer to socialize with specific individuals, and do the same relationships persist through

adolescence and adulthood? Finally, does the function of friendship in chimpanzees change with age?

Function of social bonds

For adult male chimpanzees, social bonds seem to facilitate the acquisition and maintenance of dominance rank (De Waal 1986; Goodall 1986; Nishida 1983; Watts 2002). During adolescence, however, male chimpanzees do not exhibit adult-like dominance relationships, but they do form social bonds. Social bonds may be a prerequisite for subsequent development of dominance rank relationships. Only after bonds are formed might males be able to make their way up the hierarchy. Whether the number or type of social bonds formed during adolescence predicts later dominance acquisition remains to be investigated and determined.

In addition to their importance for dominance rank relationships, social bonds may have other benefits. In several primates, including adult chimpanzees, social bonds appear to buffer individuals against stress (Crockford et al. 2008; Wittig et al. 2008; Wittig et al. 2016).

Adolescence may be a particularly stressful period for male chimpanzees, as they are traveling without their mother, entering unfamiliar parts of the territory, integrating into the adult social network, and receiving aggression from adult males (Pusey 1990). Forming bonds during this phase may be particularly important for adolescent male chimpanzees as they experience all of these new events.

The importance of adolescence

Adolescence is an important period of development in humans. The same appears to be the case in chimpanzees. It is a time of growth and change. Chimpanzees begin to sever their bond

with their mother, who has been their constant companion their whole life (Pusey 1983 1990). As I have shown, it is also a time when male chimpanzees begin to learn to navigate the social worlds of adult males. They avoid dominance interactions, but form social bonds with other males, including maternal kin, unrelated males, and their fathers. In humans, there is mounting evidence that adolescence is a key period for the development of social relationships, a sensitive period for learning how to acquire status and forge bonds (Crone and Dahl 2012; Dahl 2004). The same may be true in chimpanzees. Future work on hormonal changes during adolescence and mechanisms of bond formation in chimpanzees will provide key comparative data for understanding the development of human relationships.

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Figure 5.1. A young adult male sits behind his father. The two exhibit a strong grooming bond. To human observers, the two also bear a striking resemblance to one another.

