

Paternity and father-offspring relationships in wild chimpanzees, *Pan troglodytes schweinfurthii*

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Emily Elizabeth Wroblewski

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Anne E. Pusey, Adviser

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CHAPTER 1

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CHAPTER 2

We are indebted to Tanzania National Parks, the Tanzanian Wildlife Research Institute, and the Tanzanian Commission for Science and Technology for their permission to conduct research in Gombe National Park. We are grateful to the Jane Goodall Institute for funding long-term research at Gombe and Dr. Jane Goodall for permitting us to utilize the long-term data. We are deeply appreciative of the lab space, resources, and advice provided by Drs. Beatrice Hahn, Brandon Keele and numerous other colleagues in the Hahn laboratory at the University of Alabama-Birmingham while conducting the paternity analyses essential to this study. We thank the entire Gombe Stream Research Center staff, particularly the field assistants and fecal sample collectors, for their tireless data collection and data extraction under the direction of Drs. D. Anthony Collins, Shadrack Kamenya, and Michael Wilson. We are also deeply indebted to Joann Schumacher-Stankey for her invaluable knowledge and management of the Gombe data and database. In addition, we thank the numerous undergraduate assistants and volunteers who have entered long-term data into the database at the Jane Goodall Institute's Center

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DEDICATION

When I applied to graduate school, never in a million years could I have imagined I would have such an incredible experience, both personally and professionally. I had the opportunity of a lifetime to live and work in Tanzania for 16 months, and while it was some of the hardest work I have ever done, it was also the most rewarding. Not only did I get to observe a fascinating species in its beautiful, natural habitat, I met incredible new people, immersed myself in another culture, and learned a great deal about myself and grew immensely in the process.

There are many people to thank for me making it through this process, and, I'd like to hope, as a more critically thinking, well-rounded and better person:

A person who was instrumental in my growth as a scientist at a crucial stage is Dr. Nadean L. Brown. She was a kind, patient, and encouraging teacher, and in my time in her lab between my undergraduate and graduate years, I gained the skills that ultimately enabled me to undertake this project that was both lab and field based. I came into her lab with just a little experience and not much confidence, but under her guidance I emerged with vastly more in both respects. I cannot thank her enough for that. Then coming to graduate school, I could not have asked for any more in an adviser than I had with Dr. Anne Pusey. She gave me the room to be independent, but at the same time was always available when I needed her insight. She gave me the experience of a lifetime by taking me on as her student, and I can never fully repay her for that. I thank Anne for her trust in me, and I hope I've made her proud as her student. And of course, every one of us that studies chimpanzees owes a great debt to Dr. Jane Goodall, who not only pioneered our work but continues to support our research and crusade tirelessly on behalf of the chimpanzees we all love.

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I can always count on my siblings, Julie and John, when push comes to shove, thick or thin. And my parents - how can I ever thank them enough for raising me to do my best, take risks, and, most importantly, be a good person? Even though they may not always completely understand what I do (I'll never forget mom jokingly asking me if I was SURE my Ph.D. was not in grant-writing?), they have done everything in their power to help me achieve my every goal, and I hope they are proud of me. They have celebrated my successes whole-heartedly, and nursed me through my lowest points. I would not be here today, as I am, without them. And finally, to Connor – this is the exact point in which I fail to find the words for the person who matters most to me in this world. How can I begin to explain the way you love me so wholly and unconditionally? How can I ever fully tell you how grateful I am for always believing in me and supporting me, no matter what, through all my mistakes and crises of confidence? How can I ever thank you for always making me smile and laugh and for always keeping me focused on what truly matters in life? I am truly a better person because of you, but there are no words that are even close to the vicinity of being enough to describe what you bring to my life, and so I will just say, more than love, always.

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THESIS INTRODUCTION

One of the central questions in behavioral ecology is how cooperation and altruism evolve (Wilson 1975). Maynard Smith & Szathmary (1995) identified their evolution as one of the key transitions from single-celled organisms to complex societies. There are several hypotheses to explain the evolution of cooperation and altruism, such as group selection, reciprocity, mutualism, and manipulation, whereby some behavior involves true cooperation and altruism, while others are actually genetically selfish (Dawkins 1982; Dugatkin 1997). Kin selection is another possible explanation for the evolution of cooperative and altruistic behavior. Hamilton's seminal kin selection theory asserts that because relatives share a certain proportion of genes, individuals can increase their inclusive fitness by helping and/or not harming kin, as long as the benefits to kin outweigh the costs to the individual (1964). Since its conception, research investigating kin selection has shown it to be influential in the social structure and behavior of many species such as group-living mammals (e.g. Belding's ground squirrels, *Spermophilus beldingi*: Sherman 1977), cooperatively breeding birds (e.g. long-tailed tits, *Aegithalos caudatus*: Russell & Hatchwell 2001), amphibians (tiger salamanders, *Ambystoma tigrinum*: Pfennig et al. 1999), fish (e.g. Atlantic salmon, *Salmo salar*: Griffiths & Armstrong 2002), and eusocial insects (reviewed in Queller & Strassmann 1998). Despite the abundant evidence supporting the influence of kinship in shaping social structure and behavior in animals, the extent of its role for vertebrates continues to be debated (e.g. Chapais 2001; West et al. 2001, 2002; Clutton-Brock 2002; Griffin & West 2003).

Kinship studies have primarily focused on the discrimination of maternal kin. Among mammals, maternal kin are known to avoid mating but also to act nepotistically (Belding's ground squirrels: Holmes & Sherman 1983; spotted hyenas, *Crocuta crocuta*: Holekamp & Smale 1990; lions, *Panthera leo*: Pusey & Packer 1994; African elephants, *Loxodonta africana*: Archie et al. 2006). Compared to maternal relationships, recognition and discrimination among paternal kin have been less well-studied. Prior to DNA testing, the discrimination of paternal kin was largely unexplored in the wild because female promiscuity and lack of obvious father-offspring bonds in many species prevented paternity determination (reviewed in Widdig 2007). However there is now a small, but growing, body of evidence for the discrimination of paternal kin in wild mammalian populations, such as rodents (e.g. Holmes 1986; Wolff & Cicirello 1989; Mateo 2002), spotted hyenas (van Horn et al. 2004; Wahaj et al. 2004), and primates (Widdig 2007).

The primate order is a useful taxon in which to study kin selection and kin discrimination for two reasons. First, most primates live in permanent social groups with both kin and non-kin between which to discriminate (Pusey & Packer 1987). Second, their complex social interactions provide many opportunities to both hurt and aid others (Silk 2002). Thus, it is expected that kinship would be a basis for biasing harmful behavior, such as aggression, infanticide and inbreeding, away from relatives and altruism and cooperation towards relatives. Indeed, in primates, close maternal relatives avoid inbreeding in many species (Pusey 2005). And maternal kinship strongly influences other behavior patterns: Japanese macaques, *Macaca fuscata*, associate more with

maternal kin than non-kin (Kapsalis & Berman 1996); grooming is given preferentially to maternal kin among chimpanzees, *Pan troglodytes* (Goodall 1986); and female baboons, *Papio cynocephalus*, support maternal kin in coalitions against other females (Silk et al. 2004). Such patterns of preferential association, interaction and support are repeated across primate species (Kapsalis 2004), and vary with the degree of relatedness (Silk et al. 2004) as predicted by Hamilton's rule (1964).

It is expected that primates would attain maximal inclusive fitness by discriminating both maternal and paternal kin available in most primate social groups. However, the prevailing view has been that the discrimination of paternal kin does not occur in most species of primates (Silk 2002), because of early, non-replicable studies in captive populations that found no bias (Erhart et al. 1997; Kuester et al. 1994; Sackett & Frederickson 1987; Frederickson & Sackett 1984; Wu et al. 1980). Despite emerging data that suggest otherwise (Widdig 2007), study of paternal kin discrimination thus far has been limited. Furthermore, study has been restricted to matrilineal primate species with male-biased dispersal. Paternal kinship could also be important in a patrilineal species such as chimpanzees as males will remain with fathers and other paternal kin for life, as will females until they disperse. Thus, this study aimed to further our understanding of importance of paternal kinship in social behavior by examining the most direct paternal relationship, that of fathers and offspring, in chimpanzees. Identifying fathers and offspring and characterizing their relationship is a necessary first step on the way to testing for kin discrimination amongst non-descendent paternal kin. In Chapter 1, I first determined paternal relationships and explored patterns of male reproductive success

relative to dominance rank and the priority of access model (Altmann 1962), as well as fathers' mating strategy and age. Then in Chapter 2, I examined whether fathers showed parental investment in their juvenile and adolescent sons. Finally, in Chapter 3, I investigated whether there was inbreeding avoidance between fathers and daughters.

SPECIFIC CONTRIBUTIONS FROM CO-AUTHORS

CHAPTER 1

Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*¹

Dr. Carson M. Murray	co-wrote the introduction, reviewed earlier drafts, and assisted in statistical analysis of male strategy and female preference
Dr. Brandon F. Keele	provided technical expertise for genetic analyses and reviewed earlier drafts
Joann Schumacher-Stankey	assisted in data preparation of male mating strategies, and assisted with editing the manuscript
Dr. Beatrice H. Hahn	provided technical expertise for genetic analyses and reviewed earlier drafts
Dr. Anne E. Pusey	developed the long-term database utilized in analyses, discussed hypotheses as the paper developed, and reviewed earlier drafts

CHAPTER 2

A test of paternal kin discrimination between fathers and male offspring in wild chimpanzees, *Pan troglodytes schweinfurthii*

Jennifer Henderson	assisted with data extraction and analysis as part of an honors thesis; contributed to earlier drafts of the manuscript
Dr. Carson M. Murray	provided data on dyadic time together; reviewed earlier drafts
Leif Johnson	advised on statistical methods and inference and performed statistical tests on the data

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Dr. Anne E. Pusey

developed the long-term database utilized in analyses, discussed hypotheses as the paper developed, and reviewed earlier drafts

CHAPTER 3

Avoidance of mating by paternal kin in chimpanzees, *Pan troglodytes schweinfurthii*

Leif Johnson

advised on statistical methods and inference and performed statistical tests on the data

Alison Stanley

assisted with data extraction and analysis as part of an honors thesis

Dr. Anne E. Pusey

developed the long-term database utilized in analyses, discussed hypotheses as the paper developed, and reviewed earlier drafts

CHAPTER 1: Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*¹

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Competition for fertile females determines male reproductive success in many species. The priority of access model predicts that male dominance rank determines access to females, but this model has been difficult to test in wild populations, particularly in promiscuous mating systems. Tests of the model have produced variable results, probably because of the differing socioecological circumstances of individual species and populations. We tested the predictions of the priority of access model in the chimpanzees of Gombe National Park, Tanzania. Chimpanzees are an interesting species in which to test the model because of their fission–fusion grouping patterns, promiscuous mating system and alternative male mating strategies. We determined paternity for 34 offspring over a 22-year period and found that the priority of access model was generally predictive of male reproductive success. However, we found that younger males had higher success per male than older males, and low-ranking males sired more offspring than predicted. Low-ranking males sired offspring with younger, less desirable females and by engaging in consortships more often than high-ranking fathers. Although alpha males never sired offspring with related females, inbreeding avoidance of high-ranking male relatives did not completely explain the success of low-ranking males. While our work confirms that male rank typically predicts male chimpanzee reproductive success, other factors are also important; mate choice and alternative male strategies can give low-ranking males access to females more often than would be predicted by the model. Furthermore, the success of younger males suggests that they are more successful in sperm competition.

Keywords: chimpanzee, dominance rank, male reproductive success, *Pan troglodytes schweinfurthii*, paternity, priority of access

INTRODUCTION

Among mammals, males usually compete over access to fertile females (Trivers 1972; Cunningham & Birkhead 1998). Accordingly, there is a well-documented relationship between male dominance rank and reproductive success in many group-living species (e.g. red deer, *Cervus elaphus*: Pemberton et al. 1992; northern elephant seals, *Mirounga angustirostris*: Haley et al. 1994; African wild dogs, *Lycaon pictus*: Girman et al. 1997). In these species and numerous others, high-ranking males have higher reproductive success than their lower-ranking counterparts.

Many primates likewise show a positive correlation between male rank and reproductive success (e.g. bonobos, *Pan paniscus*: Gerloff et al. 1999; Hanuman langurs, *Semnopithecus entellus*: Launhardt et al. 2001; rhesus macaques, *Macaca mulatta*: Widdig et al. 2004; multimale gorilla, *Gorilla gorilla*, groups: Bradley et al. 2005). However, the relationship is complex, and there is variation in the strength of the association (Ellis 1995). The relationship between rank and reproductive success was formalized into the ‘priority of access’ model, which predicts how many offspring should be sired by each male based on each male’s rank and two demographic factors: the number of male competitors and the number of receptive females present for each conception (Altmann 1962). For example, if five males are in a group with two receptive females, priority of access predicts that the two highest-ranking males will each gain access to one female. Several studies have found support for this model (e.g. Japanese macaques, *Macaca fuscata*: Soltis et al. 2001; mandrills, *Mandrillus sphinx*: Setchell et

al. 2005; savannah baboon, *Papio cynocephalus*: Alberts et al. 2006) while another study in grey mouse lemurs, *Microcebus murinus*, did not (Radespeil et al. 2002). However, lemurs breed synchronously and have a dispersed social system that may make it difficult for males to successfully monitor and defend mates. The influence of breeding synchrony has been observed in other species as well; dominant male domestic cats, *Felis catus* L., were more successful when females had asynchronous estrus (Say et al. 2001).

Despite the general correlation between dominance rank and reproductive success, several factors may alter the influence of rank and explain deviations from the priority of access model. Male coalitions, female choice and alternative male mating strategies can alter male access to females (Smuts 1987) and decrease the correlation between rank and reproductive success in primates. Some females may prefer middle- or lower-ranking males, thereby enabling those males to bypass their place in the queue (e.g. rhesus macaques: Chapais 1983; ringtailed lemur, *Lemur catta*: Pereira & Weiss 1991; Japanese macaques: Soltis et al. 2001; Hayakawa 2007; chimpanzees: Stumpf & Boesch 2005, 2006). Furthermore, low-ranking males can sometimes avoid direct competition with dominant individuals by sneaking copulations, as occurs in Japanese and rhesus macaques (Berard et al. 1994; Soltis et al. 2001). The degree to which these factors are important is probably contingent upon the socioecology of the species or population.

Chimpanzees represent a particularly interesting system in which to investigate the applicability of the priority of access model. Unlike the primate species referenced above, chimpanzees live in a fission–fusion social system in which subgroups, known as

parties, are temporary within a permanent community (Nishida 1968; Goodall 1986; Boesch & Boesch-Achermann 2000). Thus, even though males can be ranked in a linear dominance hierarchy (e.g. Boesch & Boesch-Achermann 2000; Mitani & Amstler 2003; Muehlenbein et al. 2004), access to females may be dependent on party composition. For example, lower-ranking males have higher courtship success when higher-ranking males are absent (Matsumoto-Oda 1999a). Access to females could also vary across populations given differences in gregariousness and dispersal. Compared to East African chimpanzees, *P. t. schweinfurthii* (Gombe: Wrangham & Smuts 1980; Williams et al. 2002a; Murray et al. 2007), West African female chimpanzees, *P. t. verus*, are more gregarious and show comparable levels of gregariousness and similar home ranges to males (Bossou, Guinea: Sugiyama 1988; Sakura 1994; Tai National Park, Cote d'Ivoire: Boesch 1996; Boesch & Boesch-Achermann 2000; Lehmann & Boesch 2005). Additionally, while chimpanzee females generally disperse at sexual maturity (Goodall 1986; Nishida et al. 1990; Boesch & Boesch-Achermann 2000), approximately 50% of females in the main study community at Gombe National Park, Tanzania remain in their natal community with related males (Pusey et al. 1997).

Females have conspicuous sexual swellings when they are sexually receptive, and they mate promiscuously (Goodall 1986; Nishida & Hiraiwa-Hasegawa 1987). Hormonal patterns indicate that they ovulate when they are maximally tumescent (Deschner et al. 2003; Emery Thompson 2005). Males can therefore monitor female receptivity and should theoretically concentrate their mating efforts during key periovulatory periods. In fact, males show higher rates of mating during the most fertile days within a cycle, and

during conceptive cycles than during nonconceptive cycles (Deschner et al. 2004; Emery Thompson 2005; Emery Thompson & Wrangham 2008). Males also preferentially focus their mating efforts on certain individuals. A recent study from the Kanyawara community in Kibale National Park, Uganda, reported that males preferred older females and suggested that the preference for older females is selected for since they have more maternal experience and their survival may indicate higher genetic quality (Muller et al. 2007).

Male chimpanzees show three different mating strategies: (1) opportunistic, (2) possessiveness or mate guarding and (3) consortship (Tutin 1979). Consortship occurs when a male–female dyad travels alone and mates away from other members of the community. When a male has a successful consortship with a female during the fertile period of a conceptive cycle, he benefits from increased paternity certainty by eliminating competition. However, consortships are also costly since pairs often travel to the edge of the community range where they risk attack by neighboring chimpanzee communities (Goodall 1986; Gombe Stream Research Centre, unpublished data), and males involved in consortship cannot monitor other females in the group. Consortships seem to occur more frequently at Gombe (Goodall 1986) than at other study sites (Mahale: Hasegawa & Hiraiwa-Hasegawa 1990; Kibale: Watts 1998; Tai: Boesch & Boesch-Achermann 2000; Budongo: Reynolds 2005). Only 10% of offspring are conceived through consortship at Tai (Boesch & Boesch-Achermann 2000) while 21% of offspring are conceived through consortship at Gombe (Constable et al. 2001). Interestingly, only the alpha male at Tai achieved success through consortship in Boesch & Boesch-Achermann's (2000) study,

while low- to middle-ranking fathers achieved success through consortship at Gombe (Constable et al. 2001). Therefore, at Gombe, where females are less gregarious, low-ranking males may have more opportunity to lead females away on consortships.

Besides competing for fertile females through aggression and social dominance, males can also compete via sperm competition. When females copulate with multiple males, the male that produces the most sperm gains an increased chance of fertilizing a receptive female (Parker 1970). Bercovitch & Nürnberg (1996) found that rhesus macaque sires have significantly larger testes than nonsires. Sperm production generally correlates with testes size, and in diverse taxa there is a strong correlation between relative testes size and mating system, with the most polyandrous species having the largest testes (reviewed in Gomendio et al. 1998). Chimpanzees, with their highly promiscuous mating system, have particularly large relative testes size, suggesting that they experience intense sperm competition (Harcourt et al. 1981; Møller 1988; Harcourt et al. 1995). As well as individual differences in testes size, another likely factor influencing a male's success in sperm competition is age. In humans and other primates, various measures of male fertility and physiology decline with age (reviewed in: Kidd et al. 2001; Eskenazi et al. 2003; Bribiescas 2006). The promiscuously mating common lizard, *Lacerta vivipara*, also shows age-related decline in reproductive success (Richard et al. 2005), and younger bulb mite, *Rhizoglyphus robini*, males outcompete older males, siring a larger proportion of the females' eggs (Radwan et al. 2005). Thus, as long as young, even low-ranking, males secure copulations during periods of opportunistic

mating with fertile females, we might expect them to outcompete older males in sperm competition and achieve fertilization.

Here, we analyze 22 years of data to test whether male chimpanzees at Gombe National Park conform to the priority of access model. Prior work from Tai chimpanzees found that paternity patterns fit well with the model (Boesch et al. 2006). Although we also expected it to hold at Gombe, we predicted that it would not conform as closely since females are less easily monitored in this population than in more socially cohesive groups, such as the Tai population. We further predicted that deviations from the model would result from inbreeding avoidance, whereby females that remained in their natal community would mate with unrelated males that would not necessarily be predicted to have access according to the model parameters. We also expected that low-ranking males would successfully sire offspring with younger, less desirable females and through consortships, and that younger males would be more successful than older males.

METHODS

Study Population and Data Collection

Data for this study were from the Kasekela community of Gombe National Park, Tanzania. Study of this community began in 1960, and daily full-day follows on members of the community have been conducted since 1973 (see Goodall 1986, pp. 597–608 for details regarding data collection and interobserver reliability). During follows, female reproductive state (degree of sexual swelling) is noted, and data on group

composition, feeding and location are recorded every 15 min. Aggressive, submissive and mating behavior are recorded throughout the follow. We analyzed 22 years of data collected during 1984–2005. During this period, the community contained 7–12 adult males and 12–23 adult females (adult age ≥ 12 years old). We included data from 34 offspring ($N = 33$ successful pregnancies, including one set of twins) in our analyses.

Male Dominance Rank

We determined dominance rank from the direction of dyadic pant-grunts. Pant-grunts are easily audible and unidirectional submissive vocalizations that function as formal indicators of dominance (Bygott 1979; de Waal 1982). We used MatMan[©] software (version 1.1, Noldus Information Technology, Wageningen, The Netherlands) and the improved linearity test (de Vries 1995) to calculate annual dominance ranks from pant-grunt data. We included all males that were alive for at least 3 months and turned at least 12 years of age during the year. Twelve years of age is the youngest age at which males have fathered offspring at Gombe (Constable et al. 2001; this study). We found significant linearity ($P \leq 0.05$) for 17 of the 21 years in which the infants in this study were conceived using pant-grunts alone and a trend towards linearity ($P \leq 0.1$) in 1 year. For the 3 years in which there was no evidence of linearity based on pant-grunt data alone, we repeated the analysis including the outcome of dyadic agonistic interactions that had an unambiguous winner and loser. This resulted in significant linearity for 1 year ($P \leq 0.05$) and a trend towards linearity for the other 2 years ($P \leq 0.1$).

Paternity Determination and Patterns

We determined paternity for 34 of the 57 offspring born in the Kasekela community between 1984 and 2005. All sampled offspring had survived at least long enough for us to obtain a fecal sample (approximately 2 years), while most unsampled offspring were those that disappeared or died before that age. Paternities for 12 offspring were previously determined (Constable et al. 2001) but were confirmed with the genetic loci used in this study; 22 paternities (for 21 conceptions, including one set of twins) were newly determined (Appendix 1, Table A.1). All but one mother and, on average, 98.6% (range 53.3–100%) of potential fathers from within the community were also sampled (Table A.1). We conservatively included all males at least 9 years old at the time of conception as potential fathers. All offspring born from 1992 onwards (N = 25) had 100% sampling of candidate males from within the community. To account for the possibility of extragroup paternity, we included candidate males from the adjacent Mitumba community whenever genotypes were available. Samples could not be collected from some individuals because of the later habituation of this community (see Appendix 1 for details).

We used published genotypes from Constable et al. (2001) when genetic material was not available for deceased individuals. For all others, we isolated DNA from fecal samples, with the exception of one Mitumba male genotyped using tissue collected postmortem. After determining DNA concentrations using quantitative real-time PCR, we genotyped all individuals by amplifying 11 tetranucleotide microsatellite loci using

human primers according to the recommendations of Morin et al. (2001). We identified fathers using both simple exclusion and the likelihood-based program CERVUS 2.0 (Marshall et al. 1998). Detailed methods are provided in Appendix 1.

We tested for differences in the probability of siring offspring by age after controlling for male rank. For each conception we identified all candidate sires in the community that were alive at the time of conception and turned at least 12 years of age during the conception year. We assigned each candidate a rank for the conception year and categorized them by age, grouping males 12–14, 15–19, 20–24, 25–29, 30–34 and 35–39 years old. The single male over 39 years of age (aged 40) at the time of any conception was excluded from this analysis to prevent statistical bias from having only one male in an age category. We used ANOVA to test the difference in fit between two generalized linear mixed models: the first tested male age category and rank and the second tested just rank, but both controlled for repeated measures on the same male.

Testing the Priority of Access Model

Conception window

We determined the conception window for each offspring by backdating from the offspring's date of birth and identifying any swelling within the known range of gestation at Gombe (range 208–235 days; average: 229 days) (Goodall 1986; Wallis 1997). Given that the most likely time of conception is between the third and seventh day before females detumescence (Deschner et al. 2003; Emery Thompson 2005), we used this 5-day

window within each swelling as the conception window. Conception could be assigned to a single swelling cycle for all but two pregnancies. In those two cases, we included both cycles in our analyses and averaged our metrics across those cycles. We treated the twins as a single conception since only one male could monopolize the mother according to the priority of access model. Despite being nonidentical twins, both offspring were fathered by the same male (Table 1.1).

Demographic parameters

For each conception window, we determined the number of candidate males and the number of simultaneously maximally tumescent females (including the mother) present in the community during the window (Table 1.1). We calculated the average number of males and simultaneously estrous females for both cycles when mothers had two cycles of equal probability of conception.

Calculating expected success

We assigned expected success based on the priority of access model following Altmann (1962). The expected paternity for each male was based on his rank and the number of receptive females at the time of conception. For example, if there were four simultaneously swollen females and 10 adult males, the top four males of ranks 1 (alpha) through 4 would each be expected to monopolize one of those females. Those four males would each have a 0.25 chance of monopolizing the conceiving female and siring the offspring, while males ranked 5 and below would have zero likelihood of paternity.

These likelihoods were then summed for each rank to give an expected number of offspring to be sired per rank over the entire study period. We then compared the expected proportion of offspring sired to the observed proportion actually sired per rank using the Spearman rank-order correlation coefficient (α level of significance = 0.05), enabling direct comparison to the Taï population (Boesch et al. 2006). Although rank 1 is the lowest numerical rank, it is the highest (alpha) social rank, and was treated as the highest rank in the Spearman correlation.

Examining Sources of Deviation from the Priority of Access Model

Inbreeding avoidance

We modified the priority of access model to test whether close male relatives of the conceiving female in the candidate pool (sons, maternal brothers and maternal uncles) affected male reproductive success. At least one male relative was in the community for 16 of the 33 conceptions. In eight of those cases, the related male had a high enough rank to receive a likelihood of paternity that was greater than zero under the basic model parameters. These related males contributed to seven unique male–female dyadic pairs. Four dyads were maternal siblings, two were mother–son dyads, and one was a niece–uncle dyad. When a related male would have received a likelihood of paternity that was greater than zero under normal model parameters, we instead assigned the related male a likelihood of zero, shifted the greater-than-zero likelihood to the next highest ranking, unrelated male, and tested the modified model as described above.

Mating patterns

We defined the father's mating strategy following Constable et al. (2001). Consortships are difficult to identify conclusively, and so we used both a strict and a less restrictive definition. Our strict definition of consortship required either direct observation of consortship behavior in the record, or mutual absence of the mother–father pair for at least 3 consecutive days, of which at least one fell in the conception window, the coincidental departure or return of the pair, and no more than two other males absent in the same period. Our less restrictive definition was the same as that described above but without the requirement of the coincidental departure or return of the male–female dyad and without the restriction of no more than two other males also absent. We conducted analyses of fathers' strategies using both strict and less restrictive definitions.

We defined possessive behavior as when the father disrupted copulations or copulation attempts by other males, showed aggression to other males approaching the female, or otherwise showed persistent attention to the female. We considered fathers to be possessive if they showed these behaviors at least twice when the female was maximally tumescent. We examined all conceptions for evidence of possessiveness, but no instance of possessiveness, according to these criteria, coincided with consortship. If consortship or possessiveness overlapped with opportunistic mating by the father, we assigned the father's strategy to be the most restrictive of the female (i.e. consortship or possessiveness superseded opportunistic mating). If there was no evidence of consortship or possessiveness, then the father was deemed to have mated opportunistically. When we could not differentiate between two cycles for a single conception, we assigned a strategy

to each cycle individually and compared them. In both conceptions where this was the case, the strategy was the same for each cycle and therefore was the strategy assigned to the conception. Strategy was not assigned for two conceptions (SDB and TOF) because only one or no chimpanzees were followed or sighted during the mothers' swelling cycles.

To investigate how mate preferences and alternative male mating strategies influenced paternity success, we tested mother's age against father's rank, and father's mating strategy (opportunistic, possessive, consortship) against father's rank, using a linear mixed model in which we controlled for repeated measures on the same father. We assigned the mother's age as her age when conception occurred (Table 1.1). We used the same model to test mother's age against father's age category (categories as described previously), and father's mating strategy against father's age category.

RESULTS

Paternity Assignment and Distribution

We genotyped 16 of the 23 males (69.6%) that were alive for at least one conception. Despite incomplete sampling of candidate fathers, we successfully determined paternity for all 34 offspring via either simple exclusion or likelihood analysis using CERVUS 2.0 (Marshall et al. 1998). In all but one case (DIA), simple exclusion identified a single male as the only male that could have contributed the complementary set of paternal alleles given the offspring and maternal genotypes. All other candidates

had at least one mismatch, and most candidates had two or more mismatches (Table A.1). Paternities based on exclusion were also confirmed by CERVUS with at least 80% confidence, and 95% the majority of the time (Table A.1). In the case of DIA, the most likely reason neither of the two males could be excluded is because they were maternal brothers and therefore genetically very similar; however, we were still able to assign paternity using CERVUS with 75–95% certainty, depending on the simulation conditions. All 34 offspring were fathered by males within the community, and there was no evidence of extragroup paternity (see Appendix 1 for details, Table A.1).

The candidate males sired 0–7 offspring. Most males (56.5%) sired at least one offspring. The mean \pm SE number of offspring sired per male was 1.43 ± 0.42 (Table 1.2). Most of the 10 males that did not produce any offspring were present in the community as adults for the fewest number of conceptions at either the very beginning or the end of the study period, and were often quite young adults. The number of conceptions for which the males were present ranged from 1 to 33, while the percentage of conceptions obtained ranged from 0 to 33.3 (Table 1.2). There was a positive correlation between the number of conception opportunities and the number of offspring sired ($R^2_{\text{adj}} = 0.38$, $N = 23$, $P < 0.0025$; Fig. 1.1). Paternity distributions differed significantly from expected distributions based simply on the number of males per age category (chi-square test: $\chi^2_6 = 16.18$, $P = 0.013$). Males aged 15–19 years old were the most successful at gaining paternity (Fig. 1.2). Per male success dropped considerably after age 19 years and remained low, even though the average male rank continued to rise and remained relatively steady, and the average age of males during their alpha tenures in

this study was 22 (N = 6, range 19–26 years). The ANOVA test of the difference in fit between two models, one including both male age (category) and rank, and the other including just male rank, found that including male age as a variable resulted in a significantly better fit (ANOVA: $\chi^2_5 = 13.5$, P = 0.019). Thus, there was a significant difference between age categories in the probability of siring an offspring. Additionally, the probability of siring an offspring remained highest for males that were 15–19 years old, when adjusted for rank.

Priority of Access

At the time of conception, there were, on average, 10.5 candidate males (range 7–12) and 3.9 simultaneously estrous females (range 1–11) (Table 1.1). We found that paternity success decreased according to rank as predicted by the priority of access model, reaching significance in a one-tailed test and a trend towards significance in a two-tailed test (Spearman rank correlation: $r_s = 0.54$, N = 12 rank positions, one-tailed P = 0.034, two-tailed P = 0.068; Fig. 1.3). The alpha male (rank 1) secured the most offspring, siring 30.3% of the offspring, which was somewhat less than the 36.8% predicted but still 50% more offspring than the next most successful males (ranks 2 and 5). While the highest-ranking males (ranks 1–4) were less successful than predicted, males of lower ranks (5 and below) did as well as or better than predicted, and in some cases, as well as or better than males of higher rank.

Sources of Deviation

Inbreeding avoidance

Modification of the priority of access model to account for avoidance of related male candidates did not increase the explanatory power of the model. Shifting likelihoods from a related male to the next highest ranking, unrelated male resulted in a similar r_s coefficient (Spearman rank correlation: $r_s = 0.53$, $N = 12$ rank positions, one-tailed $P = 0.039$, two-tailed $P = 0.078$). However, the modification did produce a closer fit between observed and expected proportions of offspring sired by the alpha male (Fig. 1.4). Alpha males sired offspring solely with unrelated females, or 37% (10 of 27) of the offspring produced by unrelated females.

Mating patterns

Father's rank was significantly correlated with mother's age, such that lower-ranking fathers sired the offspring of younger females ($F_{1,19} = 10.5$, $P = 0.004$). Father's rank was also significantly correlated with his mating strategy when using the less restrictive definition of consortship (less restrictive: $F_{2,16} = 4.95$, $P = 0.02$; strict: $F_{2,14} = 2.52$, $P = 0.12$). Specifically, the difference between the rank of fathers using the possessive strategy and the rank of fathers using consortship was significant in the less restrictive analysis, with rank being significantly lower for fathers using consortship than that for fathers using the possessive strategy (post hoc group comparison, Tukey–Kramer adjusted: $P = 0.02$) (Fig. 1.5). Mother's age and father's strategy did not vary significantly with father's age category. Consortships were associated with 19% of

conceptions using the less restrictive definition and 9.7% of conceptions using the strict definition. Fathers were possessive in 29% of conceptions (Table 1.1).

DISCUSSION

High dominance rank carries costs such as stress, physiological and metabolic costs, and immunosuppression (Muller & Wrangham 2004; reviewed in Sapolsky 2005).

Presumably these costs are offset by higher reproductive success, and evidence for reproductive skew towards high-ranking males is widespread across mammalian taxa (e.g. African wild dogs: Girman et al. 1997; bonobos: Gerloff et al. 1999; yellow-toothed cavy, *Galea musteloides*: Keil et al. 1999; Hanuman langurs: Launhardt et al. 2001; reindeer, *Rangifer tarandus*: Røed et al. 2002; rhesus macaques: Widdig et al. 2004; multimale gorilla groups: Bradley et al. 2005). In species where multiple females can be receptive at the same time, the priority of access model predicts the order in which males have mating success. In this study, we found that male chimpanzees tend to conform to the model. However, the model had less explanatory power for the Gombe chimpanzees than was previously reported in the West African subspecies (Boesch et al. 2006). We suggest that differences in female gregariousness partially explain deviations in the model fit and that lower-ranking fathers sire offspring with younger, less desirable females and rely on the consortship strategy to secure matings.

Patterns of Paternity

As in other studies (e.g. baboons: Alberts et al. 2006; chimpanzees: Boesch et al. 2006), alpha males sired more offspring (30.3%) than all other males, but most males sired at least one offspring. Note, however, that two of the unsuccessful males (FO and ZS) were young males, and the seven ungenotyped and unsuccessful males were present for only a few of the earliest conceptions and many were very young adults. Despite the higher success of alpha males, younger males (aged 15–19 years) were more successful per candidate male than were older, often higher-ranking males, and age remained a significant predictor of male success after accounting for rank. This age-related pattern of success is similar to that found in the Tai chimpanzees, although the decline in reproductive success with age is less marked in that population (Boesch et al. 2006). The discordance of the relationship between paternity versus age and rank versus age in this study contrasts with the close fit found for baboons (Alberts et al. 2006). The age-related decline in paternity could be partially explained by male reproductive senescence. Evidence from humans shows that semen volume, count and concentration, as well as sperm motility and morphology, decline gradually as males age, starting even when men are in their 20s (reviewed in Kidd et al. 2001; Eskenazi et al. 2003). Other age-associated changes in mortality, hormone levels and sexual function in nonhuman primates follow patterns similar to those of humans and other mammals (reviewed in Bribiescas 2006). Thus the reproductive benefits of high rank may be countered by a shift in energetic investment more towards survival with increasing age (Bribiescas 2006). This age effect could be compounded in a promiscuous mating system with intense sperm competition

such as in chimpanzees (Harcourt et al. 1981; Møller 1988; Harcourt et al. 1995). Because alpha and high-ranking males copulate more frequently than low-ranking males in the periovulatory period (Matsumoto-Oda 1999a; Deschner et al. 2004), they may experience sperm depletion due to constraints on sperm production as found in Soay rams, *Ovis aries* (Preston et al. 2001). Sperm depletion in high-ranking males could enable younger, potentially more potent males to succeed in sperm competition and sire offspring even though they obtain fewer copulations in the conceptive window.

We found no evidence for extragroup paternity (EGP) in our study community despite the fact that extracommunity copulations have been observed (Goodall 1986). Similarly, EGP was not reported in the Budongo population (Uganda), although paternity for 5 of 26 offspring could not be assigned to a genotyped male (Reynolds 2005). In contrast, EGP accounted for 7.1–10.5% of the offspring born into the study communities in Tai (Cote d'Ivoire) (Vigilant et al. 2001; Boesch et al. 2006) and 25% (1 of 4 offspring) at Bossou (Guinea) (Sugiyama et al. 1993); note, however, that the socioecological context at Bossou is unusual (Sugiyama et al. 1993; Sugiyama 1999, 2004). Our results are somewhat surprising since it seems easier for females to seek copulations outside their community in Gombe, given their lower levels of gregariousness in comparison with West African chimpanzees. In addition, Gombe females might gain an advantage from seeking extracommunity copulations since so many females remain in their natal community with close relatives (Pusey et al. 1997). Nevertheless, extracommunity paternity only occurs at low levels at other sites and is

probably difficult to achieve given that intercommunity aggression is so severe (Muller 2002; Wilson & Wrangham 2003; Pusey et al. 2008b).

Priority of Access and Sources of Deviation

Patterns of paternity at Gombe generally conformed to the priority of access model (Altmann 1962), with an overall decrease in reproductive success as rank decreased, but the model had less explanatory power at Gombe ($r_S = 0.54$) than at Taï ($r_S = 0.75$; Boesch et al. 2006). In particular, lower-ranking males did better than expected. In addition to a possible advantage gained by young males in sperm competition, it seems likely that the fission–fusion grouping pattern affords low-ranking males more mating opportunities than in spatially cohesive groups such as baboons and macaques. The priority of access model may apply to chimpanzees but on a within-party basis, where lower-ranking males could have access to females when they are higher ranking than the other males in the party (Matsumoto-Oda 1999a). Additionally, the fission–fusion system may enable low-ranking males to use alternative mating strategies such as consortship more successfully. This should be true for both chimpanzee subspecies, but more so in Gombe chimpanzees since females at Gombe spend more time alone than do females of West African populations (Wrangham & Smuts 1980; Sugiyama 1988; Sakura 1994; Boesch 1996; Boesch & Boesch-Achermann 2000; Williams et al. 2002a; Lehmann & Boesch 2005; Murray et al. 2007).

Given the lower female dispersal rates at Gombe (50%) as compared to nearly complete transfer at other study sites (Gombe: Pusey et al. 1997; Tai: Boesch & Boesch-Achermann 2000; Mahale: Nishida et al. 2003; Kibale: Kahlenberg et al. 2008a), we expected that females would mate with lower-ranking males to avoid inbreeding with higher-ranking male relatives. Relatedness is influential in the reproductive success of mandrills, whereby high-ranking males sire significantly fewer offspring with closely related females (Charpentier et al. 2005). Similarly, preference for unrelated mates by female field crickets, *Gryllus bimaculatus*, decreases the probability of related individuals fertilizing their eggs (Simmons 1991). While copulations do occur between female chimpanzees and their close male relatives, male chimpanzees generally seem uninterested in mating with maternal relatives and females show resistance to their attempts (Tutin 1979; Pusey 1980; Goodall 1986; Pusey 2005). Thus far, there is only a single documented conception of an inbred offspring, between a female and her son, in the wild (Constable et al. 2001). However, when we adjusted the priority of access model to account for inbreeding avoidance of related individuals amongst the pool of male competitors, the general explanatory value of the model did not increase (standard: $r_s = 0.54$; adjusted for relatives: $r_s = 0.53$). Nevertheless, inbreeding avoidance may still be influential because the fit between the observed and the expected proportion of offspring sired improved for alpha males under the modified model. Additionally, no alpha male sired offspring with a female in the six cases where they were close maternal relatives, a pattern similar to white-faced capuchin monkeys, *Cebus capucinus*, where alpha males sired only a single offspring (of 17) with their daughters (Muniz et al. 2006). Constable et al. (2001) noted that besides resisting mating attempts by male relatives,

females might also use consortship as a means to avoid mating with relatives. Small sample size prevented us from testing whether females with relatives in the community participated in consortships more than females without relatives, but this topic warrants further investigation.

Female choice may be influential in male reproductive success in ways not just limited to inbreeding avoidance. Stumpf & Boesch (2005) found that female chimpanzees vary in their individual preferences for and rejection of particular males. This may also account for at least some of the success of low-ranking males in this study, but female choice is difficult to test, and evidence for the effectiveness of female choice in chimpanzees is conflicting. While male mating success in the periovulatory period is negatively correlated with female resistance and positively correlated with female proceptivity (Stumpf & Boesch 2006), male aggression can also coerce fecund females into mating (Muller et al. 2007). Thus, if males can effectively coerce females into mating, then it could negate the influence of female mate choice.

Although inbreeding avoidance did not influence how well the priority of access model fit our population, our results suggest that mate preferences and alternative mating strategies account for at least some of the deviations from the model. At Kibale, Muller et al. (2007) found that males prefer to mate with older females, with higher-ranking males mating more frequently with older females than lower-ranking males. Similarly, we found that higher-ranking males fathered offspring more often with older females. Thus,

if higher-ranking males focus their competitive efforts on those females, this could enable low-ranking males to mate and sire offspring with younger, less desirable females.

Consortships occurred more frequently at Gombe than at other study sites (Goodall 1986; Hasegawa & Hiraiwa-Hasegawa 1990; Watts 1998; Boesch & Boesch-Achermann 2000; Reynolds 2005). Although we found no significant effect of fathers' rank on mating strategy when we applied a strict definition of consortship, we found that consortships were used more frequently by low-ranking fathers when defined less restrictively. This finding suggests that lower-ranking males use consortships to 'steal' females from high-ranking males. Similar alternative strategies can be successful even in more socially cohesive primates. For example, lower-ranking Japanese and rhesus macaque males succeed by sneaking copulations (Berard et al. 1994; Soltis et al. 2001). The importance of alternative strategies is also evident in nonprimate species. A study of Soay rams, another polygynous and promiscuous species, found that even though the observation of a ram in consort with a ewe made him 18 times more likely to be the sire of the ewe's offspring than other candidate males, young males still sired offspring at higher rates than predicted by their consort time (Coltman et al. 1999a). Likewise, while Antarctic fur seal, *Arctocephalus gazella*, males defending a territory have a reproductive advantage, a large portion of paternity could not be attributed to the territorial male, implying that alternative strategies such as aquatic mating are important for male success (Gemmell et al. 2001).

While the priority of access model is a general predictor of reproductive success in male chimpanzees, it does not take into account recent evidence showing that primate males identify and compete more heavily for females during the females' conceptive cycles and during the periovulatory days of those cycles (longtailed macaques, *Macaca fascicularis*: Engelhardt et al. 2004; chimpanzees: Deschner et al. 2004; Emery Thompson 2005; Emery Thompson & Wrangham 2008; Hanuman langurs: Ostner et al. 2006; baboons: Gesquiere et al. 2007). The model considers all simultaneously estrous females, regardless of whether they are fertile, when making predictions for male success. However, if males can reliably distinguish between conceptive and nonconceptive cycles as well as identify the most fertile days within cycles, and higher-ranking males can outcompete others for the conceptive females, then we would expect alpha males to be even more successful than we observed, even when avoiding close female relatives. In this study of 33 conceptions, six conceptions involved temporal overlap with another female's conception window, and, for two of these, paternity of the other female's infant was unknown. Thus, we would predict that the alpha male should have gained all the conceptions with unrelated females that did not have overlapping conception windows and 50% of each overlapping pair of conceiving females, for a total of 24 conceptions (72.7%) in the study. That the alphas did considerably less well, gaining only 30.3% of conceptions, indicates either that alphas did not have complete knowledge of which females were fertile, or that they could not completely monopolize conceptive females. Given the 5-day length of the periovulatory period, it is not surprising that high-ranking males might not be able to completely monopolize a female since mate guarding (possessiveness) is probably costly in terms of the energetic

expenditure required to restrict female promiscuity (e.g. Sparkes et al. 1996), as well as in terms of the costs of having to forgo other important activities, such as foraging (e.g. Alberts et al. 1996). Such constraints on the males could be further compounded by evolutionary counterstrategies by females to conceal ovulation and confuse paternity to prevent infanticide of their offspring (reviewed in van Schaik 2000).

CONCLUSIONS

Until the advent of noninvasive genetic techniques, it was challenging to test the relationship between male dominance rank and reproductive success in wild populations, particularly in promiscuous mating systems (Hughes 1998; Di Fiore 2003). Any male, regardless of his rank, that copulates with a fertile female has a chance at siring her offspring by means of successful sperm competition. Although rank was initially thought to be unimportant in chimpanzees because males can use alternative strategies (Goodall 1986), our study confirms that male rank generally correlates with reproductive success. However, younger males had the highest success per male, and low-ranking males successfully produced offspring more often than was predicted by the priority of access model. Low-ranking fathers sired offspring with younger, less desirable females and appeared to use the consortship strategy more often than higher-ranking fathers. Thus, even though rank generally serves as a queue for males to have access to reproductive females, and males have some knowledge about female fertility, male age, mate choice and alternative male mating strategies affect patterns of male reproductive success in this

species. Future work should further explore the effect of male age, inbreeding avoidance and party composition on male mating frequency and reproductive success.

FIGURE CAPTIONS

Figure 1. 1.: Number of offspring that each adult male chimpanzee sired as a function of the number of conceptions for which he was at least 12 years of age.

Figure 1. 2.: Observed per male success by age. Number of offspring produced per male for each age category was calculated by dividing the total number of offspring produced by the number of candidate males, including fathers, in that age category during conceptions (open bars). The solid line is the mean dominance rank, and numbers beside the points of the line indicate the total number of males (both fathers and non-fathers) for which rank information was available in each category.

Figure 1. 3.: The proportion of offspring expected and observed to be sired by males of different rank. Expected proportions were determined by the priority of access model.

Figure 1. 4.: The modified proportion of offspring expected and observed to be sired by males of different rank. Expected proportions were determined by the priority of access model with modification to account for related males in the candidate pool (sons, maternal brothers and maternal uncles).

Figure 1. 5.: Average rank of fathers that achieved success through each mating strategy using the less restrictive definition of consortship. Asterisks denote statistically

significant differences in the average rank of fathers achieving success with different mating strategies. Error bars indicate $\pm 1SE$.

Table 1. 1. Paternity and demographic parameters for 33 conceptions between 1984 and 2005

Offspring	Date of birth	Mother	Mother age	Father	Father age	Father rank	Number of males	Number of estrous females	Father strategy
DIA	12/14/05	DL	18	FE	12	11	11	6	Opportunistic
BRZ	11/20/05	BAH	16	KS	23	1	11	8	Consortship
SHA	8/25/04	SR	12	WL	31	7	10	6	Opportunistic
COC	7/10/04	CD	34	FD	32	3	10	5	Opportunistic
FAM	4/18/04	FN	22	SL	20	1	10	11	Opportunistic
MAM	2/5/04	MAK	12	GL	25	8	10	1	#Consortship
GIM	1/15/04	GM	32	TB	25	2	10	3	Opportunistic
SAM	6/17/01	SA	27	FR	24	1	10	4	Possessive
SDB	6/9/01	SW	40	FR	24	1	10	4	‡
TOM	3/7/01	TA	11	KS	18	9	10	2	#Consortship
TOF	10/18/00	TTA	13	SL	16	5	10	1	‡
*FND	5/27/00	FN	18	SL	16	10	10	5	Opportunistic
ZEL	11/12/99	TZ	19	KS	17	6	10	5	Possessive
TZN	10/1/99	PI	38	FR	22	1	10	5	Possessive
FLI	7/20/98	FF	39	KS	15	6	12	5	Possessive
GLI/GLD	7/13/98	GM	27	FR	21	2	12	4	Opportunistic
YAM	7/22/98	YD	11	WL	25	8	12	3	Opportunistic
<i>FU (Fudge)</i>	12/9/96	FN	15	SL	12	10	12	2	Consortship
<i>FI (Fred)</i>	9/5/96	FF	37	FR	19	2	12	2	Opportunistic
SN	5/24/96	SA	21	AO	16	9	12	3	Opportunistic
<i>TN (Titan)</i>	7/10/94	PI	32	FR	17	5	10	3	Opportunistic
ZS	12/24/93	TZ	14	FR	16	5	10	3	Opportunistic
<i>GA (Gaia)</i>	2/14/93	GM	21	WL	19	1	11	1	Possessive
<i>FE (Ferdinand)</i>	8/19/92	FF	33	EV	39	3	11	2	Opportunistic
<i>SI (Schweini)</i>	4/15/91	SW	30	WL	17	1	11	7	Possessive
<i>CN (Conoco)</i>	1/31/91	CD	20	WL	17	1	11	7	Possessive
SR	1/25/91	SA	16	BE	20	2	11	6	Opportunistic
<i>JK (Jackson)</i>	9/16/89	JF	14	AL	21	2	11	2	Opportunistic
<i>FO (Faustino)</i>	5/8/89	FF	30	WL	15	5	9	3	Opportunistic
<i>TA (Tanga)</i>	4/22/89	PI	27	GB	24	1	9	3	Possessive

Offspring	Date of birth	Mother	Mother age	Father	Father age	Father rank	Number of males	Number of estrous females	Father strategy
<i>GD (Galahad)</i>	4/5/88	GM	16	AL	19	5	7	4	Consortship
* <i>DL (Dilly)</i>	6/17/86	(DM)	13	BE	16	9	12	1.5	#Consortship
FS	2/8/85	FF	25	GB	19	1	11	2	Possessive

Paternities from Constable et al. (2001) in italics. Parentheses indicate the genotype was unavailable for the individual. GLI and GLD were twins and were treated as a single conception.

* Number of males and estrous females were averaged across two swelling cycles.

Consortships included in the less restrictive analysis but removed in the strict analysis of father strategy.

‡ Strategy was not assigned due to lack of observations.

Table 1. 2. Total paternity success per candidate male

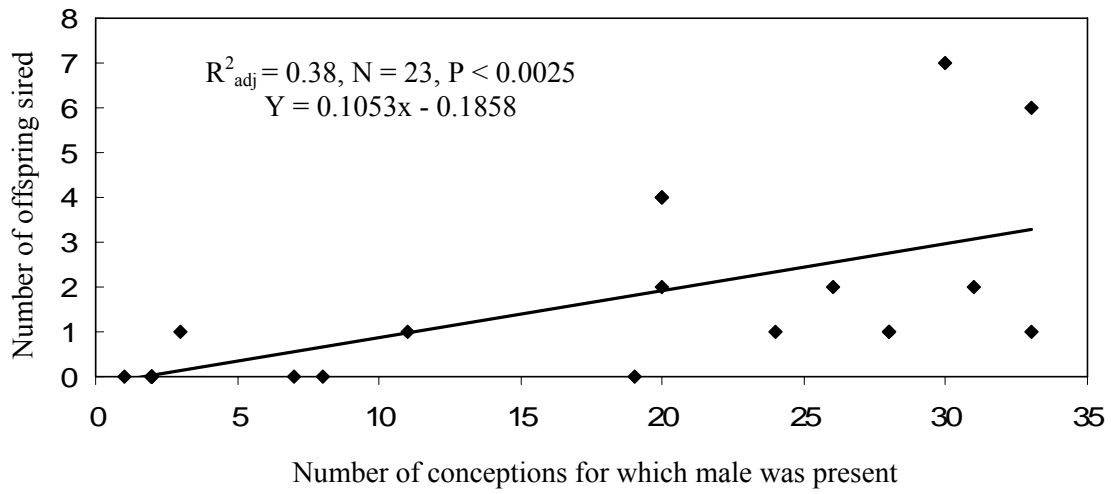
Male	Number of offspring sired	Age range during study period	Number of conceptions possible	Percent of conceptions obtained
FR	7	12-29	30	23.3
WL	6	12-33	33	18.2
KS	4	12-23	20	20.0
SL	4	12-22	20	20.0
*GB	2	20-40	31	6.5
BE	2	15-33	26	7.7
AL	2	17-31	20	10
FD	1	13-34	33	3.0
GL	1	12-28	28	3.6
TB	1	12-28	28	3.6
AO	1	12-26	24	4.2
EV	1	32-40	11	9.1
FE	1	12-13	3	33.3
PF	0	13-26	19	0
#SD	0	12-14	8	0
FO	0	12-16	7	0
ZS	0	12	2	0
#JG	0	13-15	2	0
#JJ	0	28-31	2	0
#MM	0	12-13	2	0
#MU	0	19-22	2	0
#ST	0	27-30	2	0
#CT	0	9-11	1	0

Males (N = 23) are ordered first by number of offspring sired and then by number of conceptions possible for each. Individuals in bold achieved alpha status.

Ugenotyped candidates.

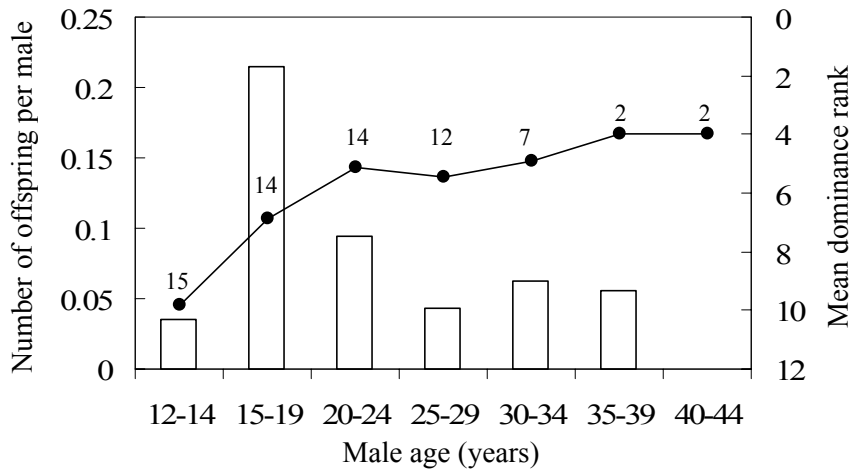
* At the end of his alpha tenure, GB sustained bad wounds to his testicles in a fight, after which he was thought to be sterile (he sired no further offspring).

Figure 1. 1. Number of offspring sired per conception opportunity



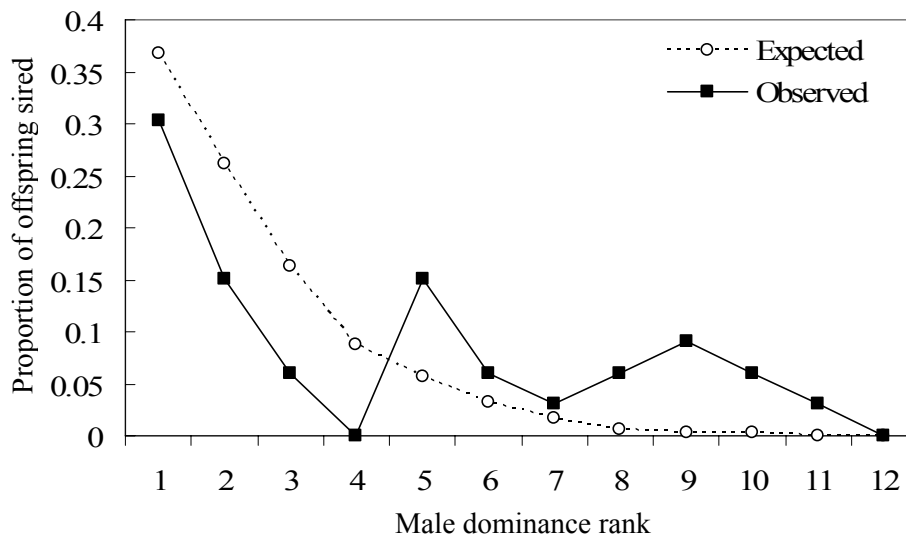
Number of offspring that each adult male chimpanzee sired as a function of the number of conceptions for which he was at least 12 years of age.

Figure 1. 2. Observed per male success by age



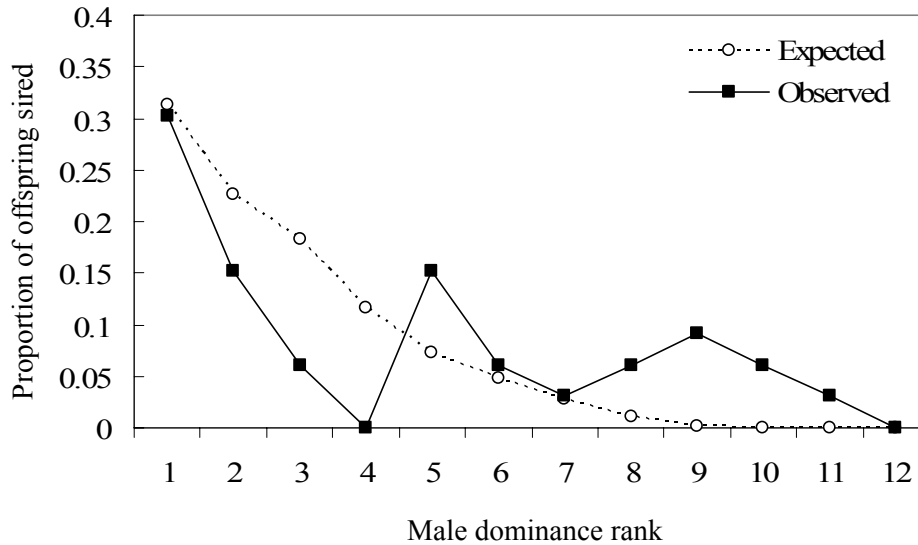
Number of offspring produced per male for each age category was calculated by dividing the total number of offspring produced by the number of candidate males, including fathers, in that age category during conceptions (open bars). The solid line is the mean dominance rank, and numbers beside the points of the line indicate the total number of males (both fathers and non-fathers) for which rank information was available in each category.

Figure 1. 3. Expected and observed offspring sired by rank



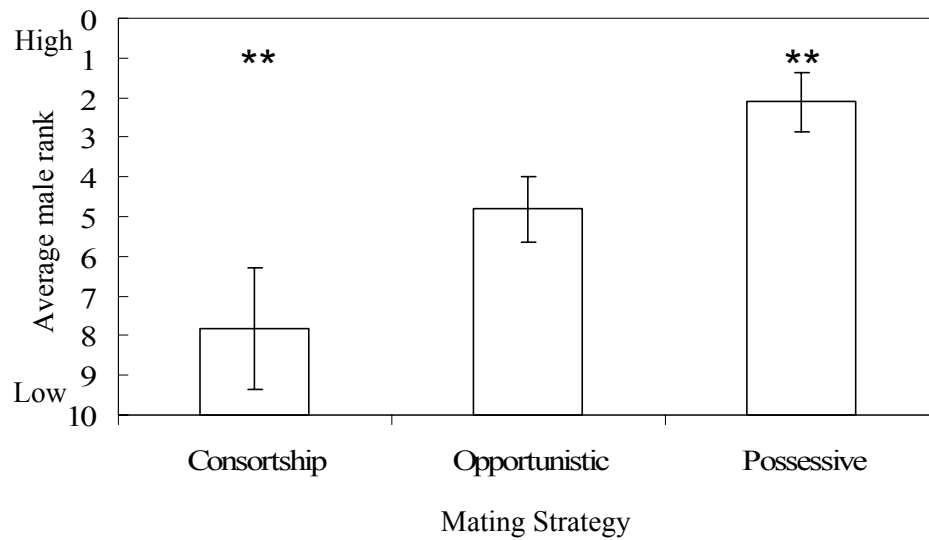
The proportion of offspring expected and observed to be sired by males of different rank. Expected proportions were determined by the priority of access model.

Figure 1. 4. Expected and observed proportion of offspring sired by rank modified for related candidate males



The modified proportion of offspring expected and observed to be sired by males of different rank. Expected proportions were determined by the priority of access model with modification to account for related males in the candidate pool (sons, maternal brothers and maternal uncles).

Figure 1. 5. Mating strategy and rank of fathers



Average rank of fathers that achieved success through each mating strategy using the less restrictive definition of consortship. Asterisks denote statistically significant differences in the average rank of fathers achieving success with different mating strategies. Error bars indicate $\pm 1SE$.

**CHAPTER 2: A test of paternal kin discrimination between fathers and male
offspring in wild chimpanzees, *Pan troglodytes schweinfurthii***

Although parental care can increase offspring survival, it may also come at the cost of parents' ability to invest in future offspring. Thus, parental care is only expected to evolve when the investment in offspring care results in increased reproductive success beyond what would be expected from securing additional offspring. In mammals, males have limited opportunity to provide care due to lengthy gestation and female lactation, and for non-monogamous species, internal fertilization is believed to reduce paternity certainty for males. However, emerging evidence suggests that fathers in some species recognize and behave differentially towards their offspring despite promiscuity. While chimpanzee males do not show obvious parental care, chimpanzees are an interesting mammalian system in which to investigate the evolution of paternal care because of their fission-fusion grouping patterns, promiscuous mating system, and unusual pattern of male philopatry. We examined the influence of kinship on interactions between adult male and juvenile and adolescent male chimpanzees in Gombe National Park, Tanzania, over an 11-year period. We did not find evidence of preferential association or interaction between young males and their fathers. However, young males did have more affiliative interactions with maternal brothers. Young males did not have significantly fewer agonistic interactions with any available kin (fathers, maternal brothers, or maternal uncles). Thus, either fathers and sons recognize each other, but the benefit of preferential interactions does not outweigh the opportunity costs, or promiscuity creates enough uncertainty for fathers to avoid the costs of misdirecting aggression towards sons and prevent more substantial investment in sons by fathers.

Key words: chimpanzee, *Pan troglodytes schweinfurthii*, paternal kin, kin recognition, kin discrimination, adolescent, juvenile

INTRODUCTION

Parental investment often has a substantial effect on offspring survival. However, parental care may cost the parent the ability to invest in future offspring (Trivers 1972). Thus, parental care should only evolve when the investment in offspring care results in increased reproductive success beyond what would be expected from future reproductive efforts (Trivers 1972; Clutton-Brock 1991). While maternal care is widespread in a variety of mammalian taxa, paternal care has been observed much less frequently (Kleiman 1977; Clutton-Brock 1991; Woodroffe & Vincent 1994). The extended gestation period and lactation by female mammals often limits males' ability to help females and increases the opportunity for them to desert females in pursuit of additional mating opportunities. Additionally, internal fertilization can result in paternity uncertainty unless males vigilantly mate-guard (Trivers 1972; Kleiman 1977; Clutton-Brock 1991). Paternal care in non-monogamous species is therefore only likely to evolve both when males can improve the fitness of their offspring and when males have a mechanism for distinguishing their offspring from unrelated individuals (Trivers 1972; Clutton-Brock 1991). However, the evolution of such mechanisms may face a strong opposing selective pressure on females for behavior that confuses paternity in order to reduce the risk of male harassment and infanticide (Hrdy 1974; van Schaik 2000; Soltis 2002).

Primates are an ideal taxon in which to study the evolution of paternal care because they vary widely in social organization, mating systems, and the degree of care

provided by males (Smuts et al. 1987). Monogamy and extensive male care have been strongly linked in primates such as siamangs, *Symphalangus syndactylus*, titi monkeys (*Callicebus spp.*), and night monkeys (*Aotus spp.*) (Whitten 1987). However monogamy does not completely explain patterns of male care in primates (Wright 1990; van Schaik & Paul 1996). Preferential relationships between assumed fathers and offspring have also been reported for polygynous gorillas, *Gorilla gorilla*, where males are extremely protective of immatures in the troop (Stewart & Harcourt 1987), and red howlers, *Alouatta seniculus*, where fathers and sons form coalitions (Pope 1990). The presence of typically only one breeding male amongst a harem of females also results in high degree of paternity certainty for both species. The influence of paternal kinship on behavior in promiscuous primates has not been well-studied, because paternity certainty is presumed to be low for males (Hrdy 1974; van Schaik 2000; Silk 2002; Soltis 2002), and it was difficult to identify fathers before the development of non-invasive genetic techniques (e.g. Constable et al. 2001).

Despite these challenges, emerging evidence from some promiscuous primate species suggests that individuals can recognize their paternal kin, as indicated by their differential interactions (Strier 2004; Widdig 2007). For example, paternal siblings have been found to preferentially interact both more affiliatively and less agonistically (rhesus macaques, *Macaca mulatta*: Widdig et al. 2001, 2002, 2006a; yellow baboons, *Papio cynocephalus*: Smith et al. 2003; Silk et al. 2006; mandrills, *Mandrillus sphinx*: Charpentier et al. 2007), preferentially form groups after fissioning (rhesus macaques: Widdig et al. 2006b; yellow baboons: van Horn et al. 2007), and avoid mating (yellow

baboons: Alberts 1999). Fathers and daughters also avoid inbreeding in white-faced capuchins, *Cebus capucinus* (Muniz et al. 2006). In addition, fathers selectively defend their offspring against aggression and infanticide in several species (Hanuman langurs, *Semnopithecus entellus*: Borries et al. 1999; Japanese macaques, *Macaca fuscata*: Soltis et al. 2000; baboons: Buchan et al. 2003), and a study of mandrills found that fathers selectively associate with offspring (Charpentier et al. 2007).

There is conflicting evidence with respect to the influence of paternal relationships on chimpanzee behavior. In most circumstances, there were no differences in the affiliative or cooperative behavior of paternal half-brothers among chimpanzees at Kibale National Forest, Uganda (Langergraber et al. 2007; Mitani 2009), with only non-significant tendencies for adult paternal brothers to maintain social bonds that lasted longer than unrelated male pairs (Mitani 2009). Similarly, there was only a weak preference for infant paternal siblings to play together more than non-kin at Taï National Forest, Côte d'Ivoire (Lehmann et al. 2006), but in contrast, Lehmann et al. (2006) found that male chimpanzees, *Pan troglodytes verus*, maintained lower levels of aggression toward females with which they had offspring and spent more time playing with their infants. However male care, particularly of infants still dependent on their mothers, can be difficult to separate from male investment in future reproduction with the mother and other benefits of “friendship” (Smuts 1985; van Schaik & Paul 1996; Nguyen et al. 2009). Male care must be biased towards offspring and increase the fitness of offspring for it to be considered true paternal investment (Trivers 1972).

There are reasons to expect that chimpanzee fathers and sons may benefit by biasing their behavior towards each other, particularly during the sons' transition into adulthood. Males do not disperse from their natal communities and therefore spend a large portion of their lives with their fathers. Over their juvenile and adolescent years, male offspring make the transition from total dependence on their mothers in infancy to complete integration into the adult male social hierarchy (Pusey 1983, 1990). During this time, young chimpanzee males often form associations with particular adult males that continue into adulthood (Nishida 1979; Hayaki 1988; Pusey 1990). Young males could benefit from these associations by observing and learning essential adult behavior and forming social bonds that ease their transition into adulthood (Walters 1987). This transition is also particularly important for young males because their future reproductive success is strongly influenced by their attainment of a high social dominance rank (Boesch et al. 2006; Inoue et al. 2008; Wroblewski et al. 2009). Williams et al. (2002b) found that sons of females that spent more time with adult males reached a higher lifetime maximum rank. Thus, special associations between fathers and young males could have important direct and inclusive fitness consequences for both if fathers facilitate the successful integration and acquisition of high rank of their male offspring.

A father's presence could have additional advantages. In baboons, a father's co-residency with his offspring was correlated with accelerated physiological maturation (Charpentier et al. 2008a), which would be another considerable means of increasing the lifetime reproductive success of offspring. Young males could also benefit from close association with fathers if fathers behave more affiliatively and less agonistically towards

them. Having fathers as a close social partner could be an important source of stress reduction, suggested by the increase in glucocorticoid levels for female chacma baboons, *Papio ursinus*, after they lost their preferred partner (Engh et al. 2006). Furthermore, strong social bonds in baboons, particularly between mothers and offspring, were associated with increased offspring survival (Silk et al. 2009). Other benefits may also include protection by the father from the aggression of others, as seen in baboons (Buchan et al. 2003), and protection from infanticide (white-footed mice, *Peromyscus leucopus*: Wolff & Cicirello 1989; alpine marmots, *Marmota marmota*: Coulon et al. 1995; Hanuman langurs: Borries et al. 1999; black rock skinks, *Egernia saxatilis*: O'Connor & Shine 2004).

Despite the potential opportunities for aiding their offspring, male chimpanzees do not appear to provide paternal care. They rarely interact with sub-adults, however, they do groom, play with, and act aggressively towards them on occasion (Nishida 1983; Hayaki 1985; Pusey 1990). While presence together in the community provides a context for preferential treatment by fathers towards offspring, there are aspects of chimpanzee behavioral ecology that could select against paternal investment. Fission-fusion grouping patterns could limit males' paternity certainty if they do not monitor a female during her entire approximately 10 day period of sexual receptivity (Nishida 1968; Goodall 1986; Nishida et al. 1990; Boesch & Boesch-Achermann 2000). Even if males do associate with the female during her entire mating period, they will likely be unable to completely prevent others from mating with the female over such an extended period, and that

promiscuity could further confuse paternity. Furthermore, males that selectively associate with their offspring after birth may lose the opportunity to monitor fertile females.

Here, we examine how kinship influences interactions between adult male and juvenile and adolescent male chimpanzees in Gombe National Park, Tanzania, over an 11-year period. We predicted that young males will have preferential relationships with their adult male relatives in the community in this critical time as they become independent from their mothers. Specifically, we predicted that young males will associate more and have biased interactions with related adult males, including fathers, compared to unrelated adults.

METHODS

Study Population and Data Collection

This study focuses on the Kasekela community of Gombe National Park, Tanzania. Study of this community began in 1960, and daily full-day focal follows of members of the community have been conducted since 1973 (Goodall 1986). Data on group composition are recorded every 15 minutes, and interactions between the focal and group members (including aggression, protection, grooming and play) are recorded on occurrence throughout the follow.

Our study examines the effect of paternal and maternal kinship on male behavior from 1995-2005. We analyzed data for nine young males (ages 5-15) for which paternity

was known, with ages 5-7 considered juvenile and ages 8-15 adolescent (Goodall 1986) (Table 2.1). The community contained an annual average of 12 (range 11-13) adult and late adolescent males at least 12 years of age, comprising 14 different individuals, during the study period. Males at least 12 years of age were considered potential interaction partners for young males during the study period because 12 years of age is the youngest age at which a male has fathered offspring at Gombe (Constable et al. 2001; Wroblewski et al. 2009). One adult male (Pax) was excluded as an interaction partner from analyses because an attack at an early age left him castrated and unable to copulate, uninterested in attaining rank, and very juvenile in his behavior (Goodall 1986; Williams et al. 2002b).

Assigning Kinship Between Males

We categorized each male dyad as one of the following four categories: maternal half-brothers, maternal uncle-nephew, father-son, or unrelated. Eight offspring had fathers that were alive during the study period, three had maternal uncles, and two had maternal half-brothers (Table 2.1). We identified maternal half-brothers and uncles from observed matrilineal pedigrees. Fathers were identified using microsatellite genotyping of DNA isolated from fecal samples (as described in Constable et al. 2001 and Wroblewski et al. 2009). While we identified one pair of full siblings and two pairs of paternal half-siblings, none of these were of age to be considered as interaction partners during the study period.

Social Behavior

While the long-term data are collected from the perspective of the focal chimpanzee, young male chimpanzees were rarely the subject of focal follows, which severely restricts the data available per dyad. Consequently, we calculated dyadic rates of aggression and interaction using all group composition and interaction data involving the individuals in the dyad regardless of the focal chimpanzee being followed. Since there are developmental changes that may influence the types and frequency of interactions between young males and adults (Pusey 1983, 1990), dyadic rates were calculated by year according to the young male's age year rather than calendar year. We only included data when they were available for both members of the dyad for the entire age year to avoid seasonal or other biases (Table 2.1).

Dyadic association

We measured the association between the adult males and young males, and the adult males and mothers of the young males, using the Simple Ratio dyadic association index (DAI) for each dyad of chimpanzee A with chimpanzee B, calculated as follows:

$$\frac{\text{Time A and B observed together}}{(\text{Time A observed without B}) + (\text{Time B observed without A}) + (\text{Time A and B observed together})}$$

(Cairns & Schwager 1987). For juvenile males between the ages of 5-7 but not yet included on the group composition checksheet for the daily follows, we used the DAI of the juvenile's mother (Table 2.1). During this developmental period juvenile chimpanzees are in almost constant association with their mothers (Pusey 1983, 1990); therefore, the mother's DAI is representative of the juvenile's association pattern.

Social interactions

We used only strictly dyadic interactions to eliminate the direct influence of other individuals.

Affiliative interactions

Affiliative interactions analyzed included grooming (given, received, and mutual (grooming is both simultaneously given and received)), play, seeking support, and protection (see Table 2.2 for definitions). Affiliative interactions were analyzed in three ways:

a) The frequency of the behavior (henceforth affiliative frequency). Rates were calculated by dividing the total number of occurrences of the behavior (bouts) by the time spent together for each dyad. Interactions had to be separated by at least 2 minutes to be counted as independent occurrences.

b) The rate of time spent grooming (given, received, and mutual) and playing (henceforth total groom and play time). Rates for each dyad were calculated by dividing the total time engaged in the affiliative behavior (duration) by the time spent together for each dyad.

c) The average time per bout for grooming and play (henceforth mean groom and play bout length). For all interacting dyads from (b) (i.e. those with rates > 0), we divided the total time spent in the behavior by the number of bouts.

Agonistic interactions

Agonistic interactions included attacks, charging displays, hits, threats, and bristling by the adult male towards the young male (see Table 2.2 for definitions). Rates for each dyad were calculated by dividing the total number of occurrences of the behavior (bouts) by the time spent together for each dyad (henceforth agonistic frequency). Interactions again had to be separated by at least 2 minutes to be counted as independent occurrences.

Age and Rank

We recorded the adult's and young male's age as their age at the beginning of the young male's age year. All adult and young males' dates of birth were known minimally to the month and year, with the exception of one adult male whose birth year was

estimated. Adult male rank was recorded as his rank at the start of the young male's age year, as previously determined by Wroblewski et al. (2009). Ranks were then categorized as high (ranks 1-4) or low (ranks 5 and below) (Table 2.3).

Statistical Analysis

The behavioral data were analyzed in five subsets: 1) DAI, 2) affiliative frequency, 3) groom and play time, 4) mean groom and play bout length, and 5) agonistic frequency. For each subset with multiple behaviors, we combined them into a single, composite rate across all behaviors for each dyadic age year because of the likelihood of a lack of independence amongst the behaviors (e.g. Alberts 1999; Smith et al. 2003) and the zero-heavy nature of the data (see Results for further description). Additionally, we analyzed the five behavioral data subsets in two ways: 1) using both juvenile and adolescent (all available) age years, as well as 2) restricting analysis to adolescent age years, when young males become independent from their mothers as they transition into adulthood (Pusey 1983, 1990).

We used several statistical models to test for differences by kin type (Table 2.4). We used a Poisson Generalized Linear Model (GLM) for the affiliative and agonistic frequency datasets. We used a binomial GLM for the DAI and total groom and play time datasets. We analyzed the mean groom and play bout length dataset with a normal Linear Model (LM). To account for repeated measures on the same individual we included an effect for the young male; due to lack of convergence with a random effect, we used a

fixed effect for the young male for all models. We also included fixed effects for the age of each member of the dyad and the adult male's rank, and a fixed effect for adolescent male age class (juvenile or adolescent) when testing all age years. The models compared the association and interaction rates of young males with related adult males to those with unrelated adult males. For each dataset the model was fit twice: once including the effect of kinship and once without. The difference between the fit of the models (and therefore the effect of kinship) was then analyzed using an F test for all GLM models, while the LM used ANOVA. When kinship had a significant effect, group comparisons were performed using the post hoc P-value Holm correction for multiple comparisons. All tests with P-values ≤ 0.05 were considered significant. We performed all statistical tests with R software (R Development Core Team 2009).

RESULTS

Dyadic Association

Young males increased their association with adult males of all kin types except maternal uncles as they aged, starting between 8 and 9 years old (Fig. 2.1; Fig. 2.2). In contrast, the association of the young males' mothers with adult males remained constant as the young male aged (Fig. 2.1; Fig. 2.3). While young males associated more with fathers and brothers and less with uncles than unrelated males, kinship did not significantly affect the DAI of young males when both juvenile and adolescent age years were included ($F_{3,390} = 0.069$, $P = 0.976$; Fig. 2.4a; Table 2.5). When we restricted analysis to adolescent age years (8-15 years old), kinship still had no effect on the DAI of

young males ($F_{3,188} = 0.096$, $P = 0.962$; Fig. 2.4b; Table 2.5). Average association rates with fathers were still higher than with unrelated males, while young males associated less with both brothers and uncles than unrelated males.

Social Interactions

Affiliative interactions

The dyadic affiliative data were zero heavy with an average of 88.7% of dyads having no recorded interactions across the six behaviors examined (range 69.5-97%), and the highest rate of any interaction type was only 0.051 bouts/hour of time together (Fig. 2.5). Grooming was the most frequent affiliative behavior. Young males groomed the adult males much more (257 recorded bouts) than they were groomed by or engaged in mutual grooming with adult males (51 and 63 bouts respectively) (Fig. 2.6). Bouts of grooming given and mutual grooming were most common with brothers. The total time spent grooming followed the same pattern. Young males spent 40.4 hours grooming adult males, most commonly brothers, but were only groomed by adult males for 7.8 hours, and spent 17.9 hours mutually grooming (Fig. 2.7). There were 70 recorded play bouts with adult males (Fig. 2.6) and 7.9 observed play hours (Fig. 2.7). Seeking support and protection occurred extremely rarely, with only 16 occurrences of the former (father: $N = 1$; brother: $N = 6$; uncle: $N = 2$; unrelated: $N = 7$; Fig. 2.6), and 14 occurrences of the latter (father: $N = 3$; brother: $N = 2$; uncle: $N = 1$; unrelated: $N = 8$; Fig. 2.6).

a) Kinship had a significant effect on the frequency of affiliative interaction between young males and adults when including all age years ($F_{3,390} = 12.019$, $P < 0.001$; Fig. 2.8a; Table 2.5). Affiliative interaction rates were significantly higher with maternal brothers than with unrelated males ($P < 0.001$), and the rate of interaction with brothers was significantly higher than with fathers ($P = 0.01$) but not maternal uncles. Affiliative interaction rates were also higher with fathers and uncles than with unrelated males but the differences were not significant. These results were similar when analysis was restricted to adolescent age years, although fathers and sons had slightly lower rates of affiliative interaction than unrelated pairs (kinship: $F_{3,188} = 8.92$, $P < 0.001$; maternal brothers: $P < 0.001$; brother-father: $P = 0.017$; Fig. 2.8b; Table 2.5).

b) Kinship had a significant effect on the total groom and play time rates between young males and adults when including all age years ($F_{3,390} = 13.694$, $P < 0.001$); Fig. 2.9a; Table 2.5). Total groom and play time rates were significantly higher with maternal brothers than with unrelated males ($P < 0.001$), but the rate with brothers was not significantly higher than that with fathers or maternal uncles, although there was a non-significant trend for brothers to have higher rates than fathers and sons ($P = 0.055$). Rates with fathers and uncles were also higher than with unrelated males but the differences were not significant. These results were the same when analysis was restricted to adolescent age years (kinship: $F_{3,188} = 10.426$, $P < 0.001$; maternal brothers: $P < 0.001$; brother-father: $P = 0.094$; Fig. 2.9b; Table 2.5).

c) Kinship did not have a significant effect on the mean groom and play bout length between young males and adults when including all age years ($F_{3,113} = 1.741$, $P = 0.163$; Fig. 2.10a; Table 2.5). Mean bout lengths were longer with maternal brothers and maternal uncles than with unrelated males, while fathers had shorter bouts than unrelated males. When analysis was restricted to adolescent age years, the effect of kinship had a trend toward significance and all kin types had longer mean bout lengths than unrelated males (kinship: $F_{3,71} = 2.456$, $P = 0.07$; Fig. 2.10b; Table 2.5).

Agonistic interactions

The dyadic agonistic data were zero heavy with an average of 91.6% of dyads having no recorded interactions across the five behaviors examined (range 82.8-97.8%), and the highest rate of any interaction type was only 0.03 bouts/hour of time together (Fig. 2.11). Attacks and displays were the most common agonistic interaction, with 90 and 87 occurrences respectively (Fig. 2.12). Hits were moderately rare, with 25 instances, while bristling and threats were quite rare, with 9 and 13 events respectively.

Kinship was not a significant predictor of the rates of agonistic interactions between young males and adult males, although agonistic interactions with all three kin types were less frequent than with unrelated males ($F_{3,390} = 0.48$, $P = 0.696$; Fig. 2.13a; Table 2.5). The result did not differ when analysis was restricted to adolescent age years, except that agonistic interactions were more frequent with fathers and maternal uncles than unrelated males (kinship: $F_{3,188} = 1.13$, $P = 0.77$; Fig. 2.13b; Table 2.5). When

behaviors were examined individually, fathers had higher rates of less severe forms of aggression, such as bristling and hits, than other males (with the exception of uncles for bristling) (Fig. 2.12). In contrast, fathers had few to no instances of the more severe forms of aggression, such as displays and attacks, compared to other males.

DISCUSSION

In this study, we did not find evidence of preferential association or interaction between young males and their fathers. Young males showed no difference in association with any kin type examined (fathers, maternal brothers and maternal uncles) compared to unrelated males. However they did have more affiliative interactions with maternal brothers, in both the frequency and the amount of time spent in those interactions. Despite having more affiliative behavior with their brothers, young males did not have significantly fewer agonistic interactions with them, or with any other kin type.

There are several reasons to regard this study as preliminary. First, the sample size of young males for which paternity was known was small. Second, the data analyzed were not collected with a focus on young males. The association rates between young males and adult males should be representative and reliable given that an individual's presence or absence in the group during the follow is relatively easy to monitor. In contrast, very few interactions were recorded. Low interaction rates are likely due both to the characteristic behavior of young males and the data collection techniques. Young males are very watchful, tend to stay towards the periphery of the group, and interact

infrequently with adult males at this developmental stage. Nevertheless, the long-term data are unlikely to record all the interactions that do occur because young males were rarely subjects of focal follows.

This is the first study of chimpanzees to examine whether father-offspring relationships exist past infancy, and particularly during adolescence, when young males are becoming independent of their mothers (Pusey 1983, 1990). The lack of significant relationship found here for this critical stage contrasts with the preferential relationship between fathers, offspring, and their mothers during infancy suggested in the Tai chimpanzees (Lehmann et al. 2006). It is possible that the preferential relationship found at Tai could simply reflect the adult male's mating effort and relationship with the mother rather than a relationship between the father and his infant (Smuts 1985; Schaik & Paul 1996; Nguyen et al. 2009). However, Buchan et al. (2003) found that baboon fathers could still distinguish their genetic offspring from unrelated offspring of females with whom they had mated during conception but had not sired, suggesting that paternal discrimination and investment in offspring can be independent of the female. Alternatively, fathers may selectively invest in their offspring when they are infants, and young and vulnerable to death, particularly from aggression and disease (Williams et al. 2008). They face high risk of aggression from conspecifics from other communities, particularly when females are at the territorial edges and encounter patrolling males (Goodall 1986; Williams et al. 2008). There is also a high degree of female resource competition (Wrangham 1980), and females have been observed to attack and kill the offspring of other females within communities (Goodall 1986; Pusey et al. 2008b). After

surviving the risks faced in infancy, the benefit of fathers assisting juvenile and adolescent offspring may not outweigh the opportunity costs, such as securing additional reproductive opportunities (Trivers 1972; Clutton-Brock 1991).

It is also possible that the effect fathers have on sons is less immediately detectable, given the subtlety of the relationship found between fathers and infants and their mothers by Lehmann et al. (2006). Young males increase their association with all adult males as they became more independent from their mothers (Pusey 1983, 1990; this study), but those young males that associate more frequently than others with adult males may attain a higher social rank (Williams et al. 2002b) and therefore greater reproductive success (Boesch et al. 2006; Inoue et al. 2008; Wroblewski et al. 2009). This may be particularly true if the young males have close relatives such as brothers or fathers present, as baboons with a father present in the group exhibited accelerated physiological maturation (Charpentier et al. 2008a). Accelerated maturation would be another substantial means of increasing the lifetime reproductive success of offspring. Consequently, as more data accumulate, it will be important to compare offspring with and without fathers and brothers present to examine whether the presence of kin in the adult male community similarly accelerates maturation in male chimpanzees, and results in higher rank acquisition and lifetime reproductive success.

While positive and negative interactions were examined collectively in this study, it will also be important to examine differences in specific behavior as data accumulates. For example, close paternal relatives may be an important source of coalitionary partners,

as found amongst paternal siblings in hyenas (Wahaj et al. 2004). In matrilineal primate species, support from mothers enables juveniles to challenge and defeat older and larger juveniles (Datta 1983a, b; Horrocks & Hunte 1983), and we might expect to see similar support in patrilineal species between fathers and sons. In addition, while the total rate of agonistic behavior may not differ between kin and non-kin, we might expect less intense forms of aggression to be directed towards kin (Kurland 1977). Such an effect was found in female bonnet macaques, *Macaca radiata*, where kin and non-kin had equivalent rates of agonistic interactions, but the severity of aggression was reduced between kin (Silk et al. 1981), and also in hyenas, where cubs directed less intense aggression towards their sires (van Horn et al. 2004). Such a difference in the intensity of aggression was suggested in this study by fathers showing lower rates of attacking and displaying at offspring than did other kin types and unrelated males.

Chimpanzee fathers were previously believed not to recognize or invest in their offspring given the promiscuous mating system, fission-fusion dynamics within communities, and lack of extensive male care in chimpanzees (Nishida 1983; Goodall 1986; Boesch & Boesch-Achermann 2000). Recent studies of chimpanzees have had conflicting results for paternal kin; fathers and offspring (Taï Forest: Lehmann et al. 2006), but generally not paternal siblings (Taï Forest: Lehmann et al. 2006; Kibale: Langergraber et al. 2007; Mitani 2009), showed paternal kin bias, adding to the debate over the influence of paternal relationships in promiscuous species. Lehman et al. (2006) showed a subtle effect whereby chimpanzee fathers maintained lower levels of aggression toward females with which they had infant offspring and spent more time

playing with their infants. Furthermore, in other promiscuously mating primate species, fathers selectively defended their offspring (Borries et al. 1999; Soltis et al. 2000; Buchan et al. 2003), associated more with offspring (Charpentier et al. 2007), and avoided inbreeding with offspring (Muniz et al. 2006). Hyena cubs, *Crocuta crocuta*, associated significantly more with fathers and directed less intense aggression towards them, while sires associated significantly more with daughters (van Horn et al. 2004). This growing evidence that fathers and offspring can recognize and treat each other preferentially challenges the hypothesis that promiscuity evolved as a female defense against infanticide (Hrdy 1974; van Schaik 2000; Soltis 2002), by confusing paternity for males and preventing paternal kin recognition and bias, and suggests that females may derive other benefits from it (reviewed in Soltis 2002; Drea 2005). However it is also possible that promiscuity may create enough uncertainty for chimpanzee fathers to avoid the costs of misdirecting aggression and infanticide towards offspring and at the same time prevent more substantial paternal investment (van Schaik 2000; Lehmann et al. 2006).

The evidence from chimpanzees and hyenas also challenges the idea that male pursuit of additional reproductive opportunities prohibits parental investment in a fission-fusion society. However, we might expect that the allocation of effort between the two male strategies of increasing fitness to vary within and between individuals, given changing socioecological circumstances and the relative benefits of each strategy. For example, a lower ranking male that is less likely to gain access to fertile females through competition with other males may invest more heavily in existing offspring than mating compared to a higher ranking male. Furthermore, in species such as chimpanzees in

which males employ different reproductive strategies (Tutin 1979), we might also expect males to vary in their parental investment according to the degree of paternity certainty associated with each strategy. Males utilizing a strategy with a higher degree of certainty, such as mate guarding or consortship, may show more paternal investment than fathers of offspring sired through opportunistic matings. Future studies will investigate this hypothesis more fully as more data become available.

The more frequent occurrence of and time spent in affiliative interactions between maternal brothers found by this study supports findings from previous studies. Preferential association between maternal brothers has been reported in chimpanzees, and they likely gain indirect fitness benefits from their association through their biased affiliative and cooperative behavior (Goodall 1986; Langergraber et al. 2007; Mitani 2009). However, we did not detect significantly increased association rates between them as found by others. This may be due to the limited data available for brothers since only two young males had brothers of age to be included in the analysis. While there is kin bias between maternal brothers (Langergraber et al. 2007; Mitani 2009; this study), interestingly, adult paternal brothers do not appear to bias behavior towards each other in most circumstances despite being of equivalent relatedness as maternal brothers (Langergraber et al. 2007; Mitani 2009). Similarly, in Lehmann et al.'s study (2006), maternal siblings played significantly more than non-kin, but there was only a non-significant tendency for paternal siblings to do so among infants. Stronger preferences for maternal than paternal siblings were also found in female rhesus macaques (Widdig et al. 2001, 2002, 2006a, b), baboons (Silk et al. 2006; van Horn et al. 2007), and hyenas

(Wahaj et al. 2004), but they still significantly preferred paternal relatives over non-kin, in contrast to chimpanzees. Such differences between equivalently related kin contradict predictions from Hamilton's rule for kin selection, which posits that the benefit of interacting differentially with kin is relative to the degree of relatedness (Hamilton 1964).

These differences in behavioral bias amongst equivalently related kin types may be explained by differences in the kin recognition mechanism used to distinguish them. Maternal siblings are typically familiar with each other via their extended, shared association with their mothers (Goodall 1986; Rendall 2004), in addition to having other, probable phenotypic mechanisms available to differentiate maternal siblings from unrelated individuals (Parr and de Waal 1999; Charpentier et al. 2008b; Loisel et al. 2008). Familiarity through age proximity has been implicated as a cue to bias behavior towards paternal siblings when male reproductive skew creates age cohorts of individuals sired by the same male (Alberts 1999; Widdig et al. 2001; Silk et al. 2006). While chimpanzees do have a high degree of reproductive skew (Boesch et al. 2006; Inoue et al. 2008; Wroblewski et al. 2009), studies of chimpanzees at Kibale National Park, Uganda (Ngogo: Langergraber et al. 2007) and Mahale National Park, Tanzania (M group: Inoue et al. 2008) found that skew was not extreme enough for males within an age cohort to be significantly more related to each other than to males outside of their cohort. Thus age is not likely as reliable of an indicator of paternal sibship, as in baboons and rhesus macaques (Widdig et al. 2001; Silk et al. 2006), and could explain the difference in maternal and paternal sibling bias in chimpanzees in absence of an alternative recognition mechanism. However, at least in hyenas, paternal siblings cooperated more and fought

less than non-kin even though neither were previously familiar, suggesting a phenotype matching mechanism can evolve for paternal siblings (Wahaj et al. 2004).

Studies have also attributed differences in sibling preference by kin type to variability in rank similarity (Widdig et al. 2001, 2006a) and the size and composition of kin networks (Silk et al. 2006). Nevertheless, when relatives do not behave differentially towards each other, as with chimpanzee paternal siblings, it is difficult to determine whether this is because they are unable to recognize those relatives as kin or whether it is because the benefits are not significant enough to outweigh any costs associated with recognition or interaction (Hamilton 1964; Kapsalis & Berman 1996; Belisle & Chapais 2001). In white-faced capuchins, fathers and daughters avoid inbreeding and therefore must have a mechanism of kin recognition (Muniz et al. 2006). Nevertheless, while maternal siblings have high rates of affiliative interactions in this species, paternal siblings do not (Perry et al. 2008). This pattern of kin bias is like that of chimpanzees, and suggests that either the mechanisms for father-offspring recognition do not enable recognition of paternal siblings, or they can recognize paternal siblings but just do not bias behavior towards them.

CONCLUSIONS

Taken together, the evidence from chimpanzees suggests that paternal kin discrimination is socioecologically contextual. Previous studies have shown that fathers may have some preference for their infant offspring, but there is no apparent preference between paternal

siblings. However, this preliminary study further shows that there is no biased behavior by fathers towards their juvenile and adolescent sons, though more data are clearly needed. Future studies need to determine what accounts for this variation in kin preference. Studies need to clearly test for the presence and absence of kin recognition mechanisms as well as identify the type of mechanisms used to bias behavior towards different types of kin, such as fathers and offspring versus paternal siblings. Future studies also need to clearly quantify the costs and benefits to preferential behavior between kin, as we would only expect kin recognition and bias to evolve when the benefits exceed the costs. Such variation in costs and benefits may account for paternal investment in infants versus older offspring. And finally, given that fathers sometimes appear to be able to recognize offspring in promiscuous mating systems, we need to identify the adaptive value of female promiscuity.

FIGURE CAPTIONS

Figure 2. 1.: The average DAI for each young male-adult male kin type by age class, and the average DAI between the young males' mother and adult male by young male age class. Error bars indicate ± 1 SE.

Figure 2. 2.: The distribution of DAIs for each young male-adult male dyad by the young males' age year for each kin type.

Figure 2. 3.: The distribution of dyadic DAIs for between the young males' mothers and adult males by the young males' age year.

Figure 2. 4.: Coefficient of the difference between the DAI of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates association is higher for the related dyads than the unrelated dyads while a negative coefficient indicates association is lower for the related than the unrelated dyads. Error bars indicate ± 1 SE.

Figure 2. 5.: The distribution of dyadic young male-adult male frequencies of affiliative interaction for all six affiliative behaviors.

Figure 2. 6.: The average frequencies of affiliative interactions for each behavior by kin type for a) all young male age years, and b) strictly adolescent age years. Error bars indicate ± 1 SE. Grooming direction is from the perspective of the young male (i.e. Grooming given is grooming given by the young male to the adult male).

Figure 2. 7.: The average total groom and play time for each behavior by kin type for a) all young male age years, and b) strictly adolescent age years. Error bars indicate ± 1 SE. Grooming direction is from the perspective of the young male (i.e. Grooming given is grooming given by the young male to the adult male).

Figure 2. 8.: Coefficient of the difference between the affiliative frequency of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates rates are higher for the related dyads than the unrelated dyads while a negative coefficient indicates rates are lower for the related than the unrelated dyads. Error bars indicate ± 1 SE. Asterisks denote statistically significant differences from unrelated dyads (above the bar) or between kin types (above the line connecting them).

Figure 2. 9.: Coefficient of the difference between the total groom and play time of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates rates are higher for the related dyads than the unrelated dyads while a negative coefficient indicates rates are lower for the related than the

unrelated dyads. Error bars indicate ± 1 SE. Asterisks denote statistically significant differences from unrelated dyads.

Figure 2. 10.: Coefficient of the difference between the mean groom and play bout length of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates rates are higher for the related dyads than the unrelated dyads while a negative coefficient indicates rates are lower for the related than the unrelated dyads. Error bars indicate ± 1 SE.

Figure 2. 11.: The distribution of dyadic young male-adult male frequencies of agonistic interaction for all five agonistic behaviors.

Figure 2. 12.: The average frequencies of agonistic interactions for all young male age years for each behavior by kin type (L-R in order of increasing severity). Error bars indicate ± 1 SE.

Figure 2. 13.: Coefficient of the difference between the agonistic frequency of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates rates are higher for the related dyads than the unrelated dyads while a negative coefficient indicates rates are lower for the related than the unrelated dyads. Error bars indicate ± 1 SE.

Table 2. 1. Data available for individual young males by age year

Young male	Age year											Adult relatives available		
	5	6	7	8	9	10	11	12	13	14	15	Father	Maternal brother	Maternal uncle
FE	X ^M	X ^M	X	X	X	X	X	X				(EV)	FD, FR, FO	
FO		X	X	X	X	X	X	X	X	X	X	WL	FD, FR	
FU	X ^M	X ^M	X ^M									SL		FD, FR, FO, FE
GD			X	X	X	X						AL		GB, GL
JK		X	X	X	X							AL		
SN	X ^M	X ^M	X ^M									AO		SL
TN	X ^M	X ^M	X	X	X	X						FR		
TZN	X ^M											FR		
ZS	X ^M	X ^M	X ^M									FR		

Available data are indicated by X. The mother's DAI was used for some juvenile age years, indicated by X^M. Juvenile age years are in bold. Relatives were considered available if the relative was ≥ 12 years of age during the young male's age year.

() Paternity was known for FE, however his father died before the start of the study period.

Table 2. 2. Behavioral definitions

Category	Behavior	Definition
Affiliative	Seeking support	After receiving aggression, the young male: 1) embraced a third-party adult male, 2) approached another adult male who was not the aggressor while screaming/crying, or 3) reached towards/stared at an adult male and back at the aggressor
	Protection	An adult male showed overt aggression towards the young male's opponent in a dispute or the adult male established affiliative physical contact with the young male after a dispute with a third party (e.g. Buchan et al. 2003)
Agonistic	Bristle	Piloerection
	Threaten	Single instances of non-contact aggression, such as head jerks or arm-raises
	Hit	Single instances of aggressive physical contact
	Display	A prolonged sequence of aggressive behavior, such as charging and shaking branches, in absence of physical contact
	Attack	Repeated aggressive physical contact

Table 2. 3. Number of dyadic age years for analysis distributed by the dominance rank of the adult male and his relationship with the young male

	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
Father	9	1	3	1	3	2	1	3	1	5	2	1	0	32
Brother	14	6	4	2	0	0	4	0	2	6	1	1	0	40
Uncle	2	2	2	3	0	1	3	0	3	3	1	1	0	21
Unrelated	17	31	31	29	29	39	30	34	27	11	26	4	5	313
Total	42	40	40	35	32	42	38	37	33	25	30	7	5	406

Ranks in bold (1-4) were categorized as High and ranks 5 and below were categorized as Low in the statistical models.

Table 2. 4. Summary of statistical models used to test each dataset

Young male years	DAI	Affiliative frequency	Groom and play time	Mean groom and play bout length	Agonistic frequency
All (juvenile and adolescent)	Binomial GLM (F test)	Poisson GLM (F test)	Binomial GLM (F test)	LM (ANOVA)	Poisson GLM (F test)
Strictly adolescent	Binomial GLM (F test)	Poisson GLM (F test)	Binomial GLM (F test)	LM (ANOVA)	Poisson GLM (F test)

GLM is a Generalized Linear Model, and LM is a Linear Model. The test used to compare the difference in fit between models with and without kinship is inside parentheses.

Table 2. 5. Results summary for age years analyzed for each measure

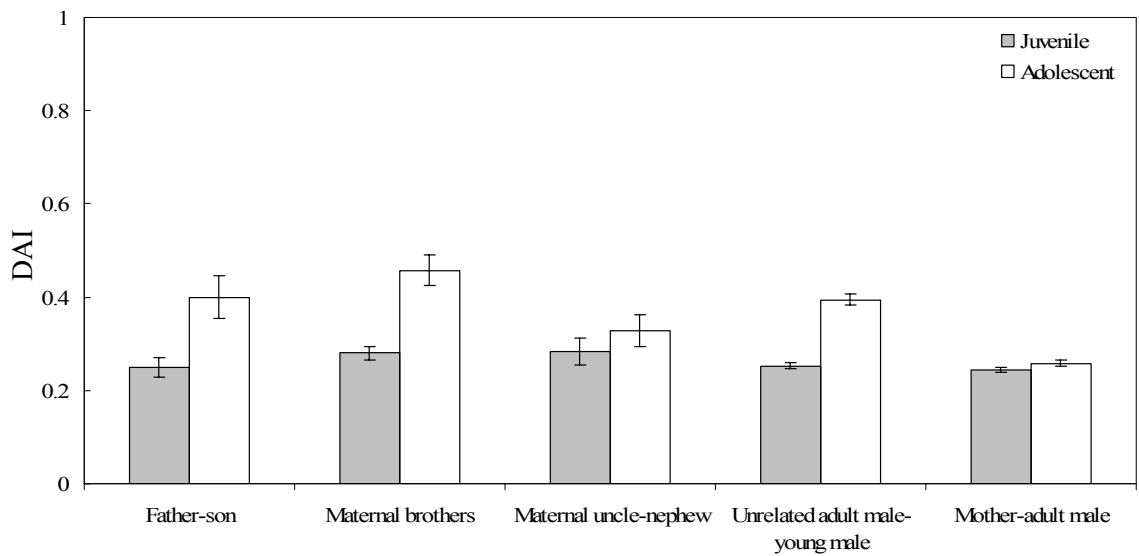
	All Age Years			Adolescent Age Years		
	Father	Brother	Uncle	Father	Brother	Uncle
DAI	+	+	-	+	-	-
Affiliative frequency	+	+*	+	-	+*	+
Groom and play time	+	+*	+	+	+*	+
Mean groom and play bout length	-	+	+	+	+	+
Agonistic frequency	-	-	-	+	-	+

+ Interaction for the kin type was increased compared to unrelated dyads.

- Interaction for the kin type was decreased compared to unrelated dyads.

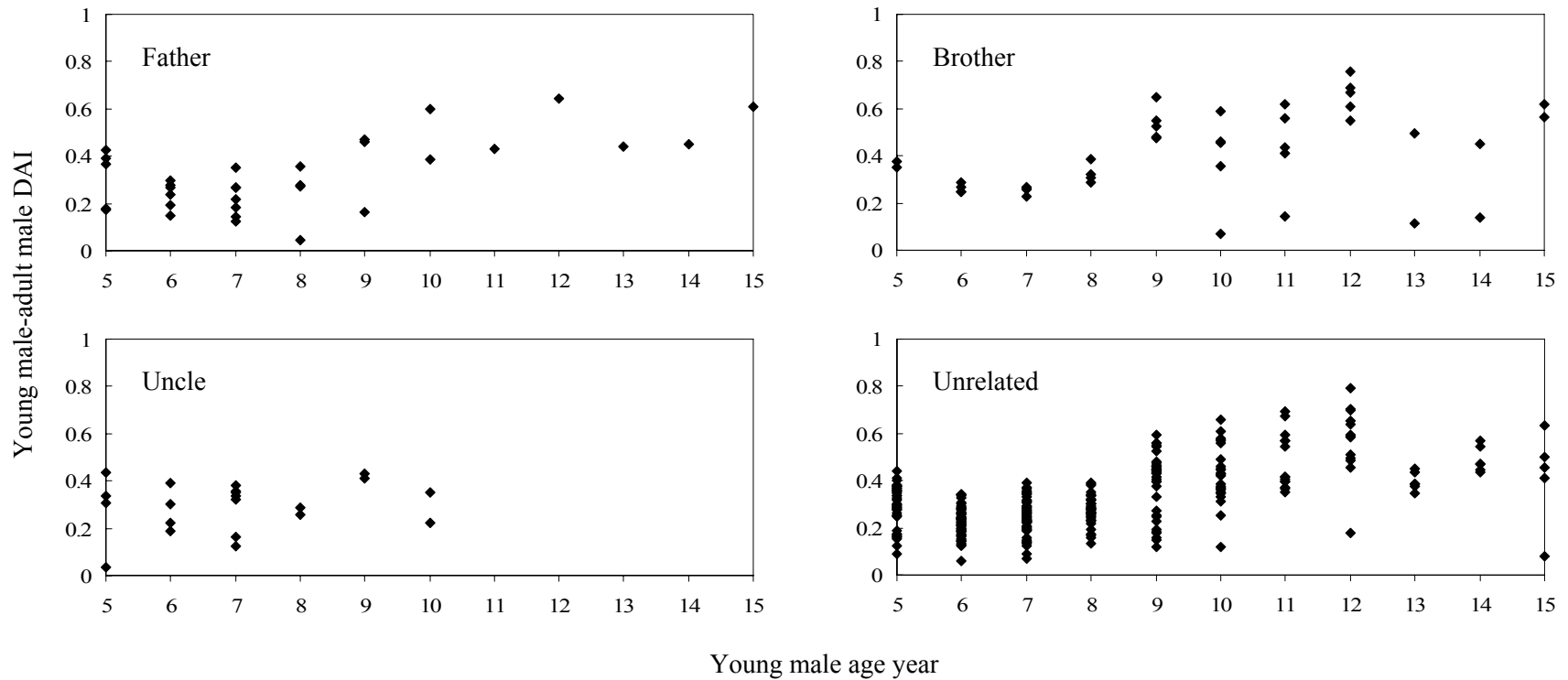
* Result was significantly different compared to unrelated dyads.

Figure 2. 1. Average DAI by age class and kin type



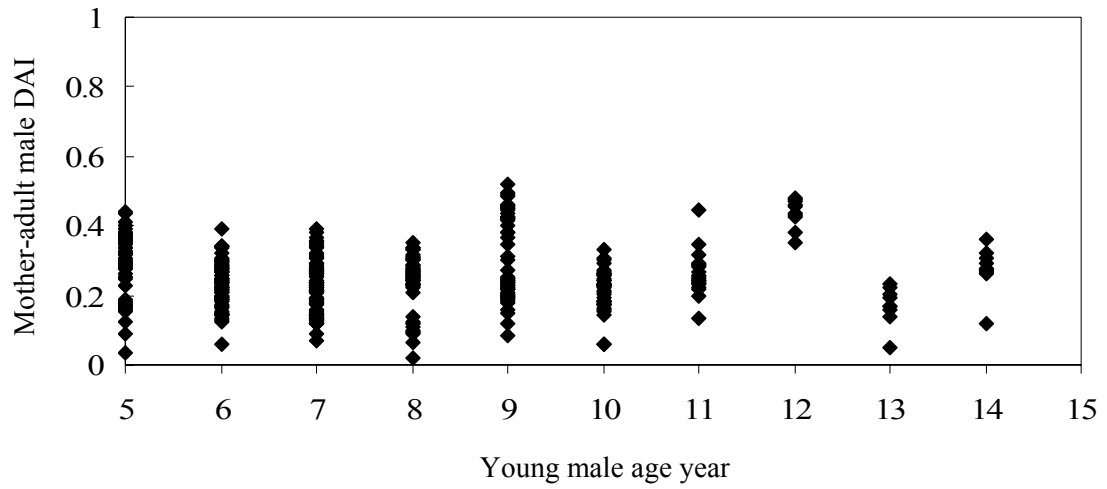
The average DAI for each young male-adult male kin type by age class, and the average DAI between the young males' mother and adult male by young male age class. Error bars indicate ± 1 SE.

Figure 2. 2. Young male DAI distribution by age year and kin type



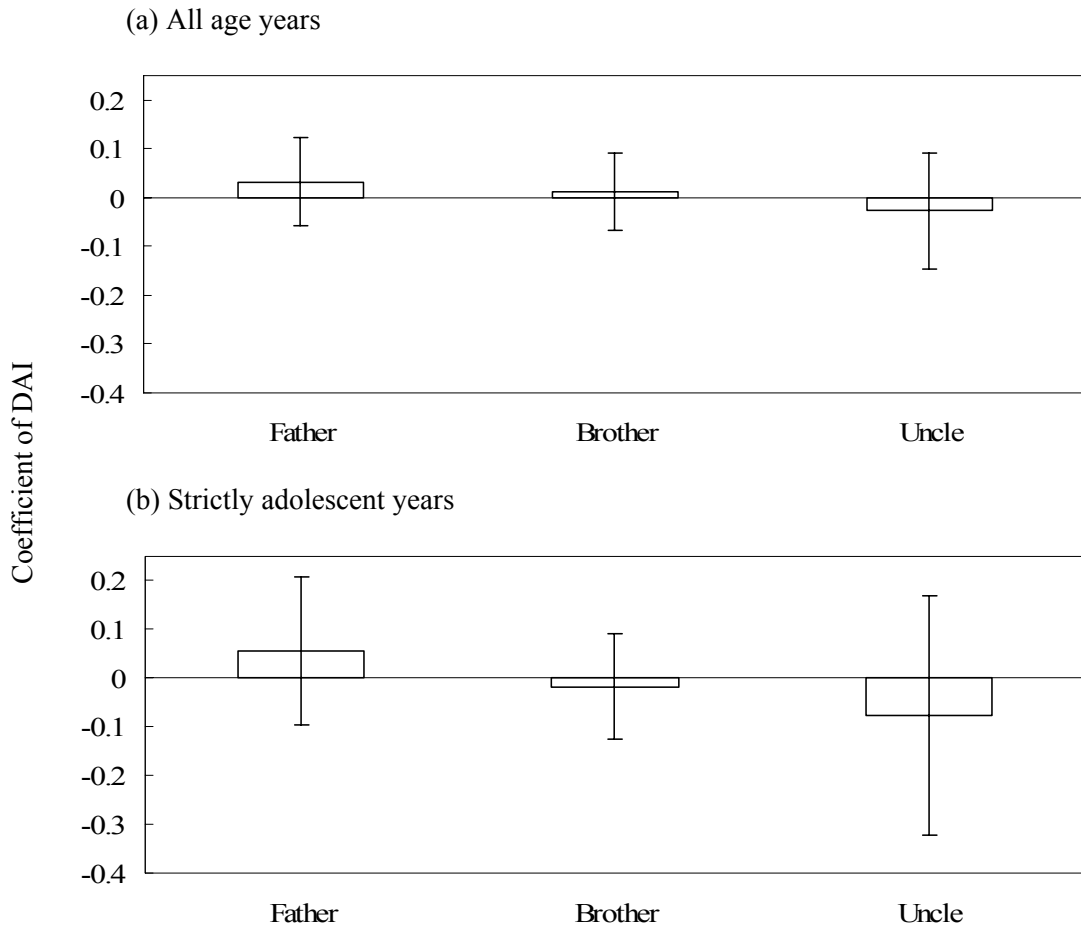
The distribution of DAIs for each young male-adult male dyad by the young males' age year for each kin type.

Figure 2. 3. Distribution of mothers' DAI with adult males by young male age year



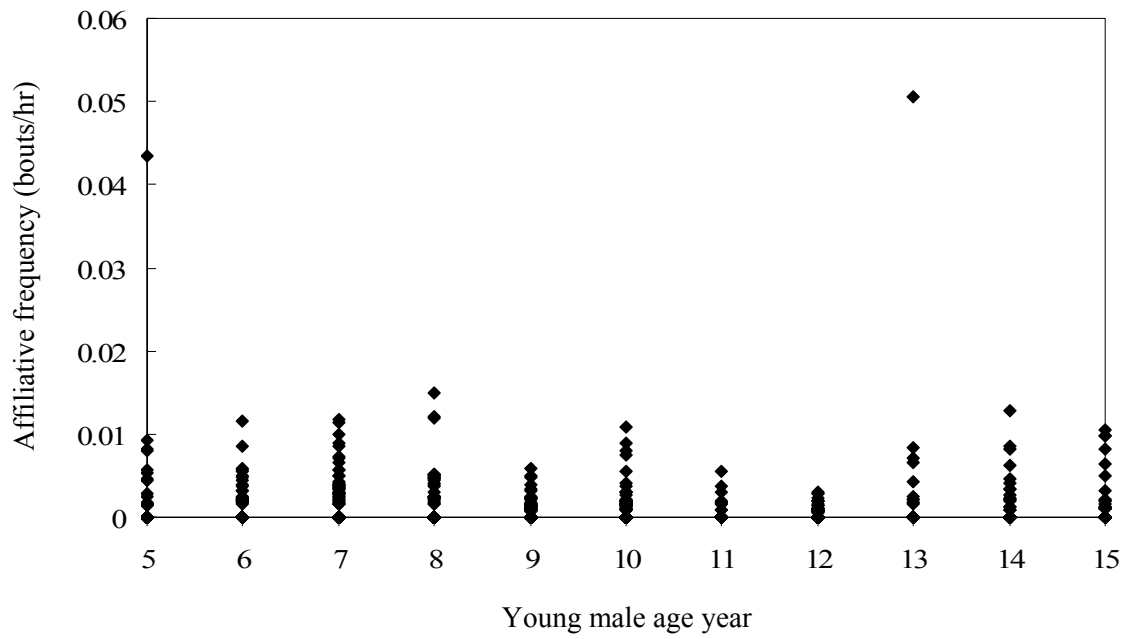
The distribution of dyadic DAIs for the young males' mothers and adult males by the young males' age year.

Figure 2. 4. Coefficient of DAI by kin type



Coefficient of the difference between the DAI of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates association is higher for the related dyads than the unrelated dyads while a negative coefficient indicates association is lower for the related than the unrelated dyads. Error bars indicate ± 1 SE.

Figure 2. 5. Distribution of affiliative frequency by age year



The distribution of dyadic young male-adult male frequencies of affiliative interaction for all six affiliative behaviors.

Figure 2. 6. Average affiliative frequency by behavior and kin type

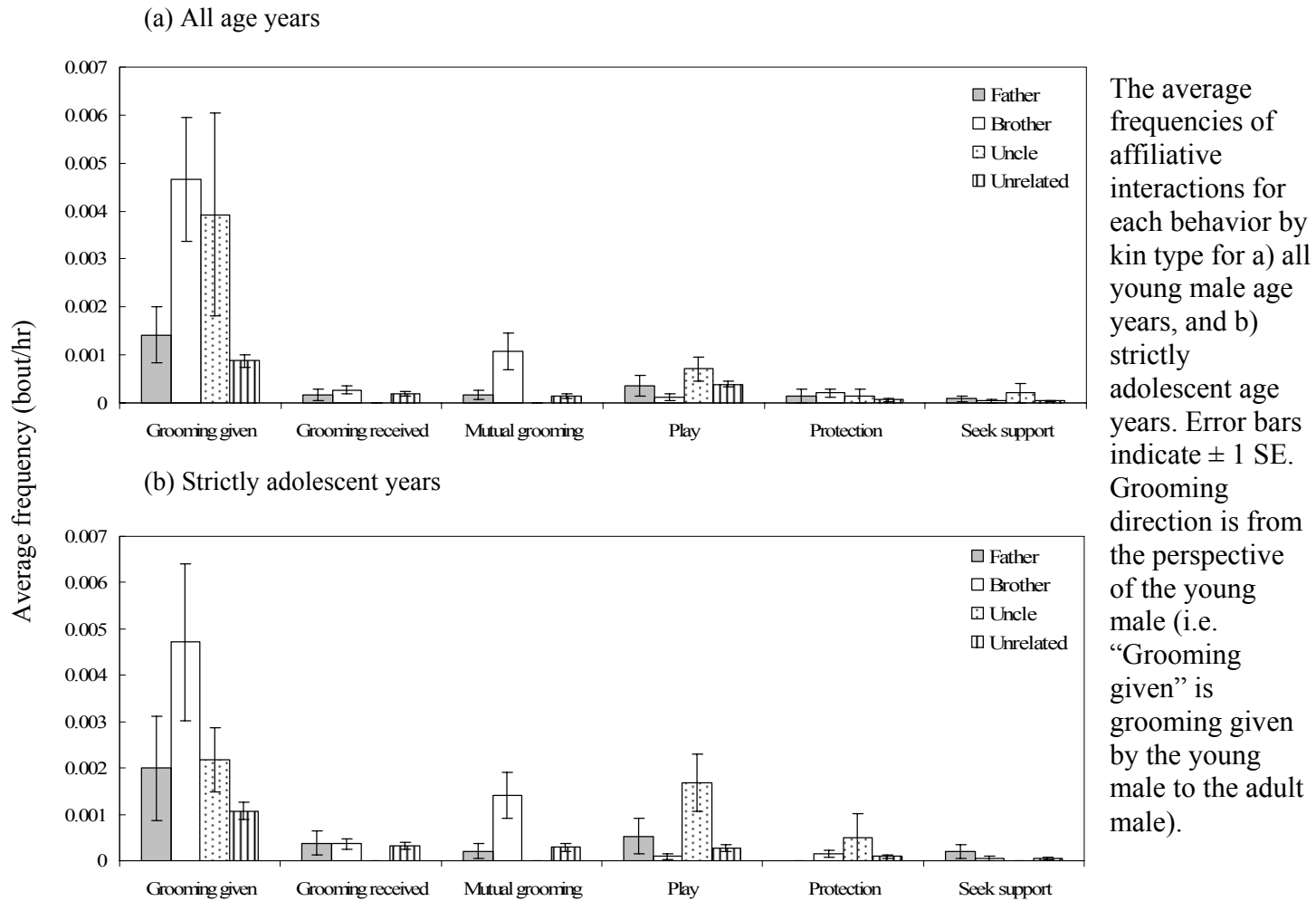
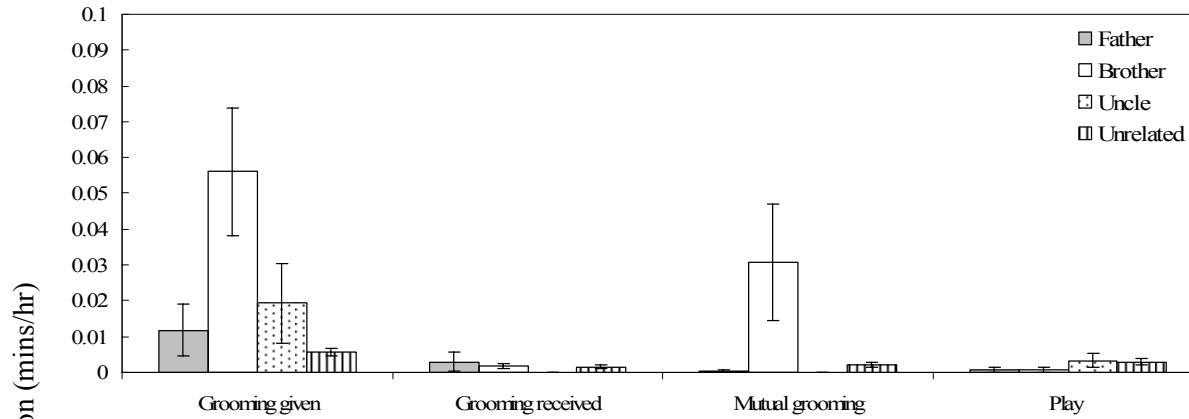
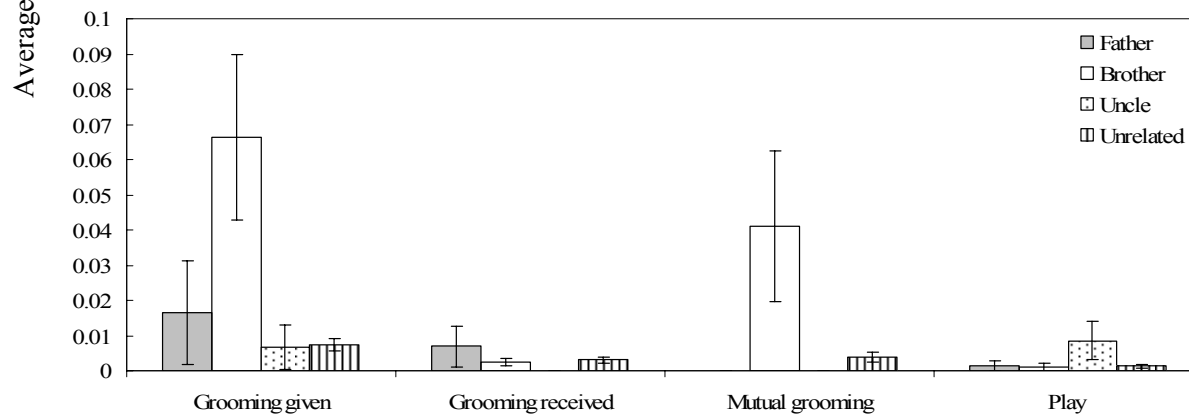


Figure 2. 7. Average total groom and play time by behavior and kin type

(a) All age years

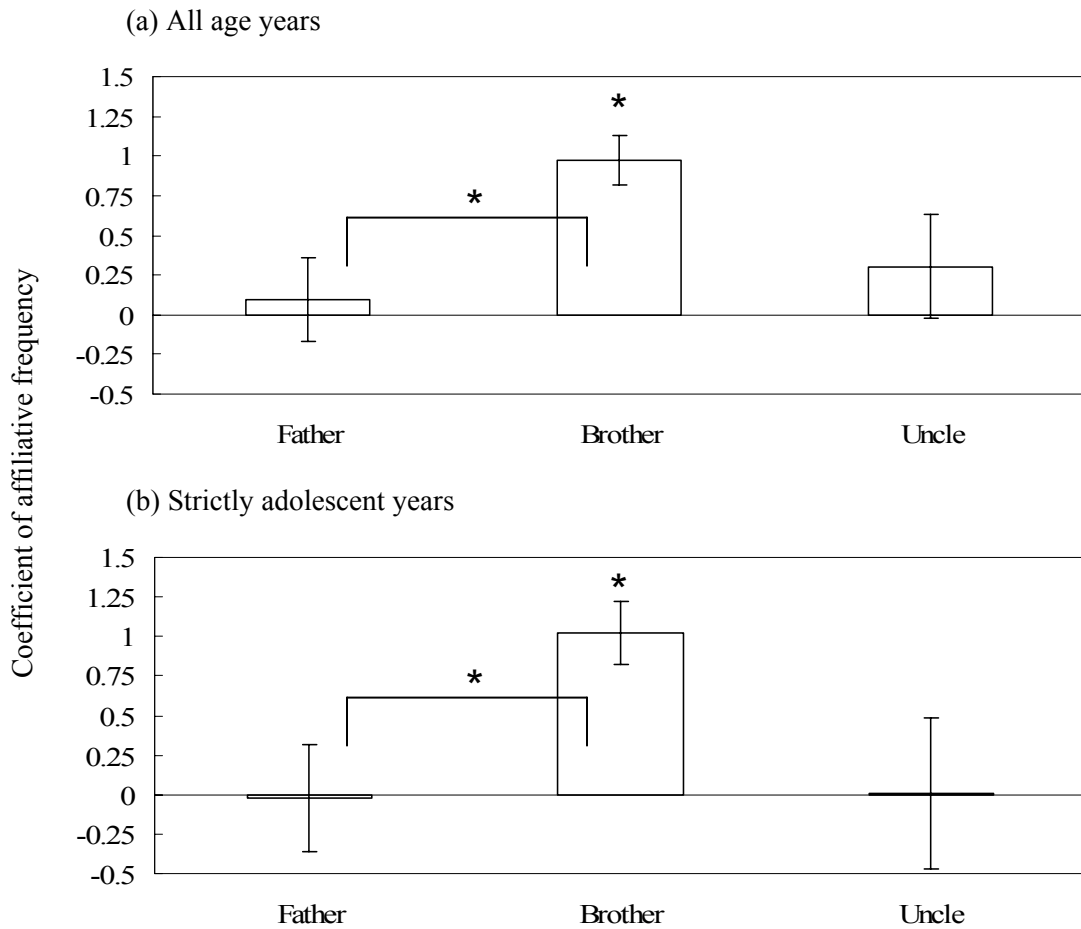


(b) Strictly adolescent years



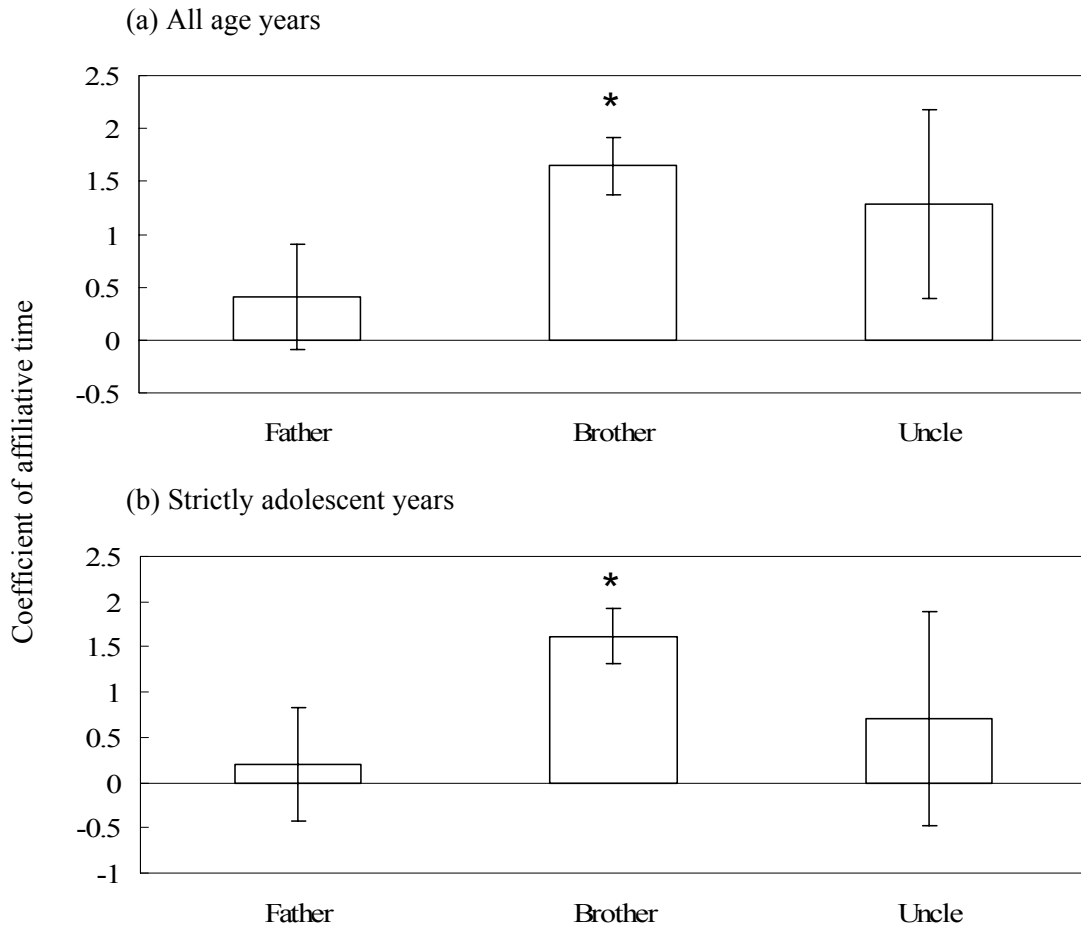
The average total groom and play time by kin type for a) all young male age years, and b) strictly adolescent age years. Error bars indicate ± 1 SE. Grooming direction is from the perspective of the young male (i.e. “Grooming given” is grooming given by the young male to the adult male).

Figure 2. 8. Coefficient of affiliative frequency by kin type



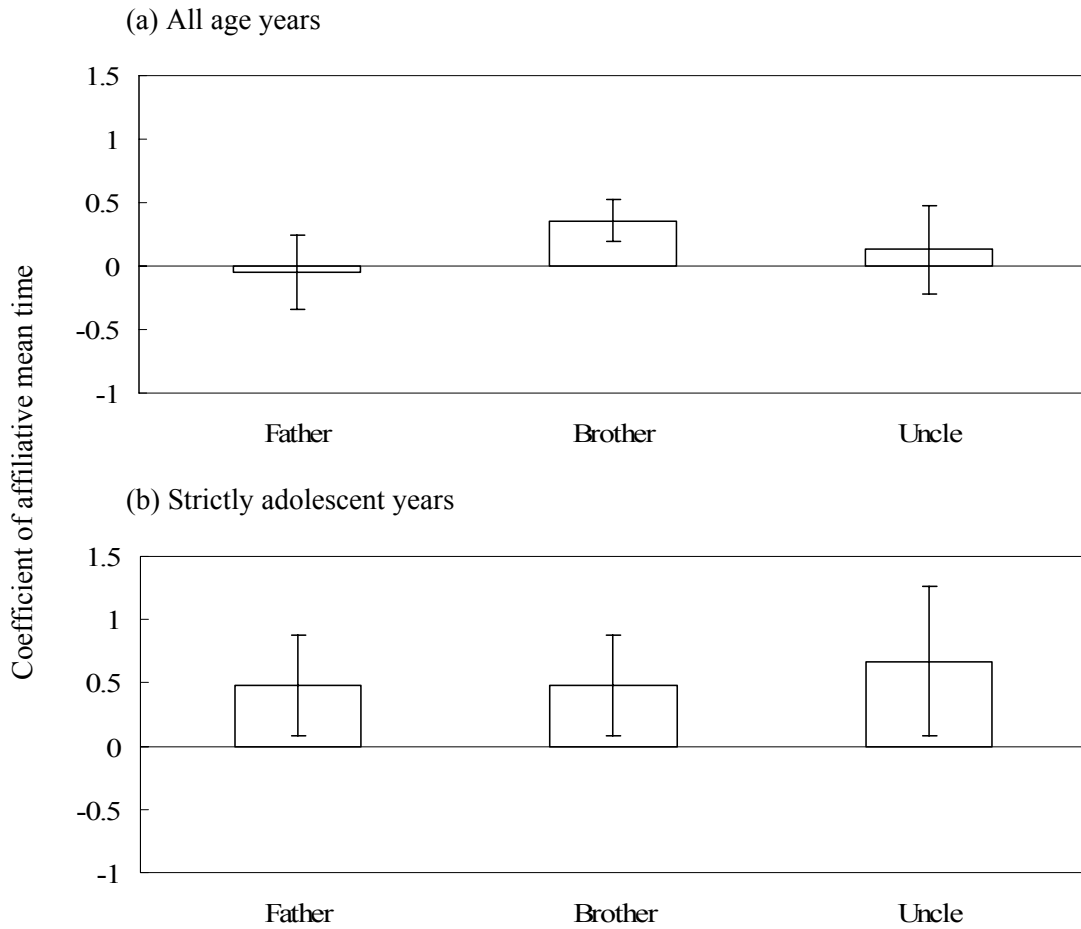
Coefficient of the difference between the affiliative frequency of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates rates are higher for the related dyads than the unrelated dyads while a negative coefficient indicates rates are lower for the related than the unrelated dyads. Error bars indicate ± 1 SE. Asterisks denote statistically significant differences from unrelated dyads (above the bar) or between kin types (above the line connecting them).

Figure 2. 9. Coefficient of total groom and play time by kin type



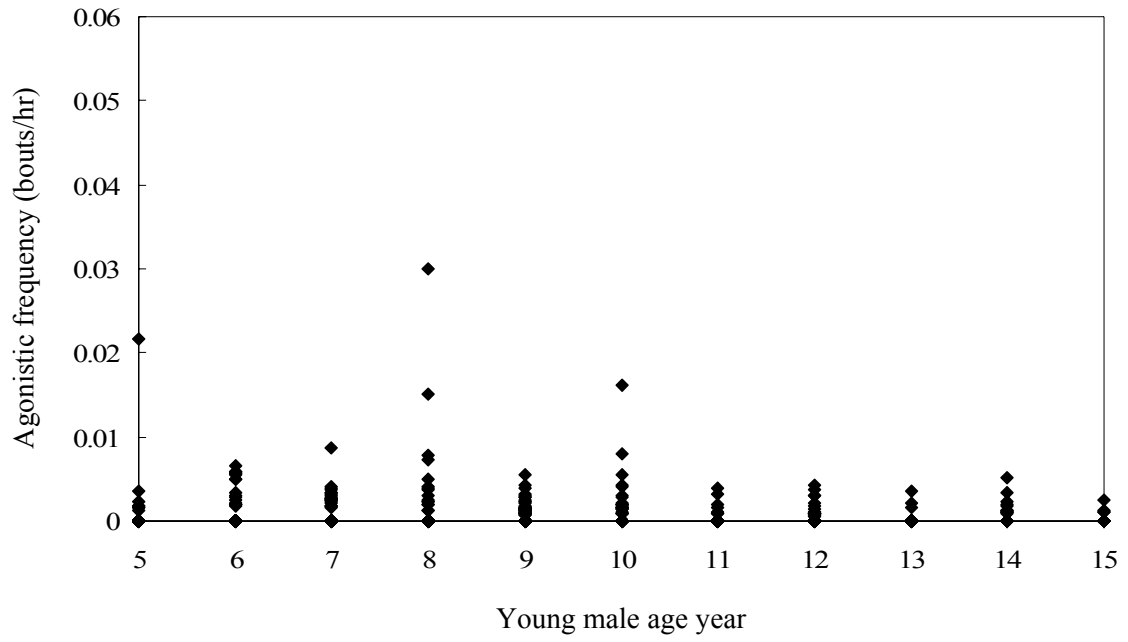
Coefficient of the difference between the total groom and play time of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates rates are higher for the related dyads than the unrelated dyads while a negative coefficient indicates rates are lower for the related than the unrelated dyads. Error bars indicate ± 1 SE. Asterisks denote statistically significant differences from unrelated dyads.

Figure 2. 10. Coefficient of mean groom and play bout length by kin type



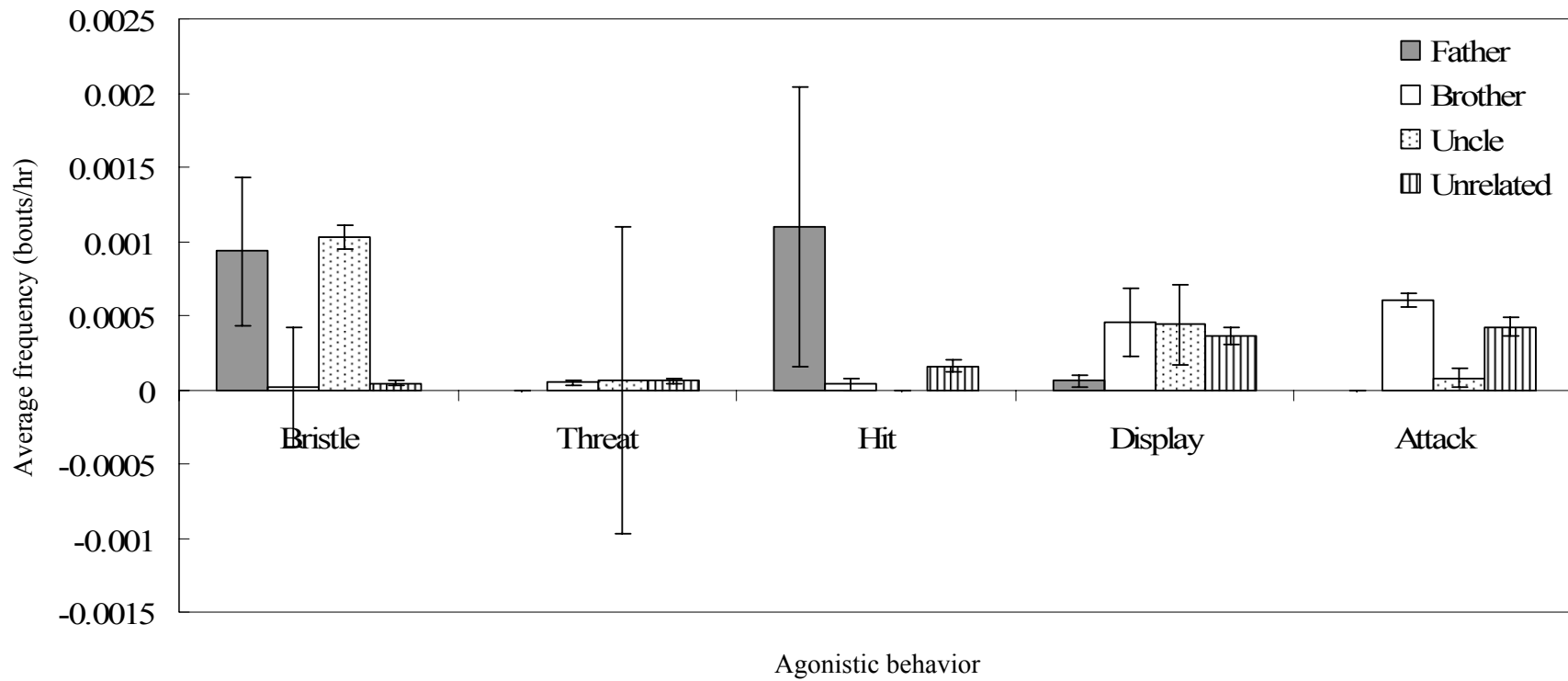
Coefficient of the difference between the mean groom and play bout length of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates rates are higher for the related dyads than the unrelated dyads while a negative coefficient indicates rates are lower for the related than the unrelated dyads. Error bars indicate ± 1 SE.

Figure 2. 11. Distribution of agonistic frequency by age year



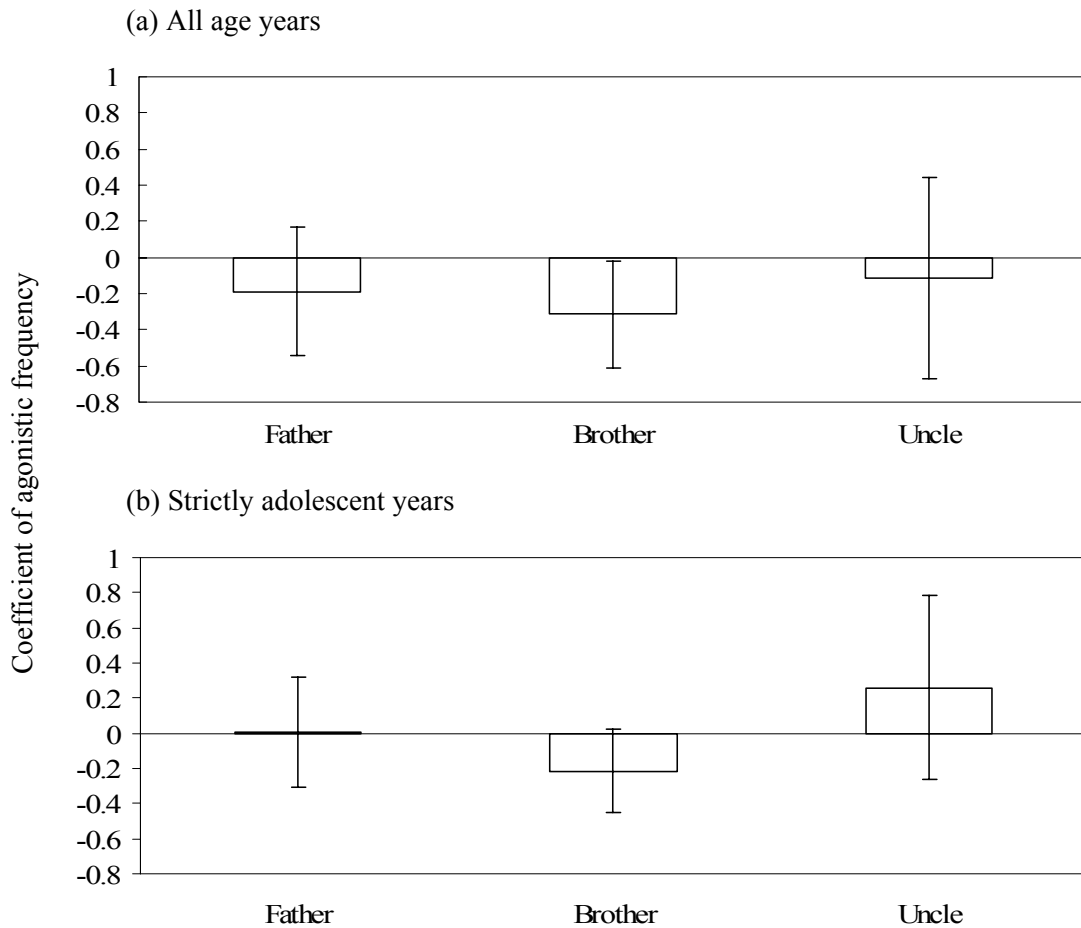
The distribution of dyadic young male-adult male frequencies of agonistic interaction for all five agonistic behaviors.

Figure 2. 12. Average agonistic frequency by behavior



The average frequencies of agonistic interactions for all young male age years for each behavior by kin type (L-R in order of increasing severity). Error bars indicate ± 1 SE.

Figure 2. 13. Coefficient of agonistic frequency by kin type



Coefficient of the difference between the agonistic frequency of related dyads and unrelated dyads for a) all young male age years, and b) strictly adolescent age years. The average rate for unrelated dyads is set as the x-axis. Thus a positive coefficient indicates rates are higher for the related dyads than the unrelated dyads while a negative coefficient indicates rates are lower for the related than the unrelated dyads. Error bars indicate ± 1 SE.

**CHAPTER 3: Avoidance of mating by paternal kin in chimpanzees, *Pan troglodytes*
*schweinfurthii***

Inbreeding can result in significant costs to fitness. In mammals, selection has likely favored inbreeding avoidance through a variety of mechanisms, and avoidance has been well-documented in many species, particularly amongst maternal kin. However, when individuals remain in their natal group, they also face the risk of mating with paternal relatives. We would expect selection to favor avoiding kin regardless of whether they are maternal or paternal relatives. The Kasekela community of Gombe National Park provides a natural opportunity to test for avoidance of mating and inbreeding among paternal kin in chimpanzees because approximately 50% of its females do not disperse from their natal community. We examined the influence of kinship on mating behavior of the Gombe chimpanzees over a 27-year period. We found a trend of less successful copulation between females and their fathers and significantly less successful copulation between females and their maternal brothers. Behavioral patterns suggest that it was mostly the males' effort that led to the sexual activity between relatives, while, in contrast, females were primarily responsible for mating avoidance with their relatives. Thus daughters appear to avoid their fathers, but fathers do not appear to avoid their daughters. Promiscuity may therefore effectively confuse paternity for males, while selection may have favored recognition and avoidance of fathers by daughters because the costs of inbreeding are likely higher for females than males. Alternatively, fathers may also recognize their daughters, but the costs of inbreeding are not sufficiently high for males to avoid mating with them.

Keywords: chimpanzee, inbreeding, mate choice, paternal kin, kin recognition, *Pan troglodytes schweinfurthii*

INTRODUCTION

Kin recognition can be adaptive by maximizing benefits from interacting affiliatively with kin as well as minimizing the costs from detrimental interactions, such as aggression and inbreeding. The result of inbreeding is an increase of homozygosity amongst the offspring's genome, which can allow deleterious recessives to be expressed or decrease the heterozygote advantage (Wright 1921; Crow 1948; Charlesworth & Charlesworth 1987). The costs of increased homozygosity at loci affecting fitness, known as inbreeding depression (Charlesworth & Charlesworth 1999), are well-documented and include reduction in reproduction (e.g. red deer, *Cervus elephus*: Slate et al. 2000; Amos et al. 2001; Coho salmon, *Oncorhynchus kisutch*: Gallardo et al. 2004), survival (e.g. primates: Ralls & Ballou 1982; red-cockaded woodpeckers, *Picoides borealis*: Daniels & Walters 2000), growth (e.g. wolves, *Canis lupus*: Laikre & Ryman 1991; mandrills, *Mandrillus sphinx*: Charpentier et al. 2006), immunocompetence (e.g. Soay sheep, *Ovis aries*: Coltman et al. 1999b; song sparrows, *Melospiza melodia*: Reid et al. 2003; ring-tailed lemurs, *Lemur catta*: Charpentier et al. 2008c), and resistance to environmental stress (e.g. song sparrows: Keller et al. 1994; fruit flies, *Drosophila melanogaster*: Reed et al. 2002). These effects of inbreeding depression can have considerable consequences in wild populations, such as increased risk of extinction, (e.g. Crnokrak & Roff 1999; butterflies, *Melitaea cinxia*: Nieminen et al. 2001; O'Grady et al. 2006; fruit flies: Reed et al. 2002).

Because of the often dramatic costs associated with inbreeding depression, selection likely acts strongly to favor mechanisms to avoid mating amongst close relatives. Indeed, inbreeding avoidance is observed in a variety of species in which close relatives are available as potential mates (e.g. meadow voles, *Microtus pennsylvanicus*: Bollinger et al. 1993; savannah sparrows, *Passerculus sandwichensis*: Wheelwright & Mauck 1998; field crickets, *Gryllus bimaculatus*: Bretman et al. 2003; Cunningham's skinks, *Egernia cunninghami*: Stow & Sunnucks 2004; African elephants, *Loxodonta Africana*: Archie et al. 2007). In mammals, several mechanisms of inbreeding avoidance are possible. Sex-biased dispersal from the natal social group or range can be a means of avoiding mating with close relatives (Pusey 1987; Clutton-Brock 1989; meadow voles: Bollinger et al. 1993). If individuals remain in their natal group with kin, they may recognize and avoid close relatives as mates (reviewed in Pusey & Wolf 1996; zebrafish, *Danio rerio*: Gerlach & Lysiak 2006; African elephants: Archie et al. 2007), or they may delay their maturation or reproduction while relatives are present (e.g. Pusey & Wolf 1996; montane voles, *Microtus montanus*: Berger et al. 1997; Damaraland mole-rats, *Cryptomys damarensis*: Cooney and Bennett 2000; meerkats, *Suricata suricatta*: O'Riain et al. 2000). In addition, there can be post-copulatory inbreeding avoidance, whereby female promiscuity enables sperm from unrelated males to out-compete that from related males, or even in absence of sperm competition there may be cryptic female choice or reproduction may be less successful due to genetic incompatibility (field crickets: Bretman et al. 2003; yellow-toothed cavy, *Galea musteloides*: Keil & Sachser 1998; Stockley 2003; reviewed in Tregenza & Wedell 2000).

Primates are an interesting taxon in which to investigate inbreeding avoidance because of their variety of mating systems and social grouping and dispersal patterns. There is considerable evidence that maternal relatives within the same social group avoid mating (reviewed in Pusey 2005). Conversely, studies of paternal kin are limited, particularly in multi-male groups where females mate promiscuously, paternity certainty is presumed low for males (Trivers 1972; Hrdy 1974; Clutton-Brock 1991), and paternity is not readily known to researchers. However, we should expect selection to favor avoiding kin as mates, regardless of whether they are maternal or paternal relatives. There is some evidence that fathers and daughters recognize and avoid mating with each other in multi-male societies. Father-daughter avoidance in olive baboons, *Papio anubis*, was suggested by reduced sexual activity between females and males when males were potential fathers (Packer 1979), and in Thomas langurs, *Presbytis thomasi*, nulliparous females only dispersed when their fathers were present (Sterck et al. 2005). There is also genetic evidence suggestive of father-daughter inbreeding avoidance in white-faced capuchins, *Cebus capucinus* (Muniz et al. 2006), and chimpanzees, *Pan troglodytes schweinfurthii* (Wroblewski et al. 2009). Few to no offspring were sired by fathers despite the fact that fathers were often high-ranking, and high-ranking males were otherwise known to sire the majority of offspring in these species. Similarly, in mandrills, the dominant males had significantly fewer conceptions when related to the female at $R = 0.5$, including fathers and daughters (Charpentier et al. 2005), and in rhesus macaques, *Macaca mulatta*, offspring were sired between fathers and daughters less often than expected from random mating (Smith 1995). There is also evidence that paternal siblings can avoid inbreeding. Alberts (1999) found that yellow baboon, *Papio cynocephalus*,

paternal siblings had less affiliative and sexual behavior during sexual consorts than non-kin, although they were not less likely to consort.

In chimpanzees, females typically disperse when they reach sexual maturity, but the degree to which they do so varies widely (Gombe: Pusey et al. 1997; Tai: Boesch & Boesch-Achermann 2000; Mahale: Nishida et al. 2003; Kibale: Kahlenberg et al. 2008a). Maternal kin are known to avoid mating when they remain in the same community after the females become sexually mature, although the degree to which they do is variable (Tutin 1979; Pusey 1980; Goodall 1986; Constable et al. 2001; Pusey 2005; Stumpf et al. 2009). Nonetheless, there has only been a single documented inbred offspring produced, between a mother and son (Constable et al. 2001). However, when females remain in their natal group, they also face the risk of mating with paternal relatives, although it is not known whether they avoid them. The chimpanzees of Gombe National Park provide a natural opportunity to test for avoidance of mating and inbreeding among paternal kin in chimpanzees because approximately 50% of females stay in their natal community (Pusey et al. 1997). Thus, here we use 27 years of data to test whether fathers and daughters recognize and avoid each other as mates. We predicted that related pairs, including fathers and daughters, would show less sexual behavior than unrelated pairs. Specifically, we predicted that, compared to unrelated dyads, related pairs will have:

- 1) less frequent sexual activity and less successful copulation
- 2) less frequent initiation of copulation and less responsiveness (copulation) following initiation
- 3) less frequent interference in copulations between females and other males by

males related to the female

4) less affiliative behavior such as association and grooming

METHODS

Study Population and Data Collection

This study is of the Kasekela community of Gombe National Park, Tanzania. Study of these chimpanzees began in 1960, and members of the community have been followed in daily full-day focal follows since 1973 (Goodall 1986). Field assistants record group composition data every 15 minutes. Grooming involving the focal chimpanzee is consistently recorded on occurrence. Data on conspicuous interactions between all group members, including aggression, submission, and mating, is also recorded on occurrence throughout the follow.

Our study examines the effect of paternal relatedness on mating behavior from 1980-2006. We analyzed data for all eight sexually mature females for which paternity was known, although the father of one female died before she reached maturity (Table 3.1). The community contained an annual average of 11.2 (range 7-13) adult and late adolescent males at least 12 years of age, comprising 25 different individuals during the study period. Males were included in the analyses as potential mates when they were at least 12 years of age by the end of the last year of the mating window (described below) because 12 years of age is the youngest age at which a male has sired offspring at Gombe (Constable et al. 2001; Wroblewski et al. 2009). We excluded one male (Pax) from

analyses because his castration at a young age left him unable to and uninterested in copulating and very juvenile in his behavior (Goodall 1986; Williams et al. 2002b).

Assigning Kinship Between Dyads

We categorized each female-male dyad as father-daughter, maternal or paternal half-siblings, maternal or paternal uncle-niece, or unrelated. We identified maternal relatives from observed matrilineal pedigrees, and fathers were identified using microsatellite genotyping of DNA isolated from fecal samples (as described in Constable et al. 2001 and Wroblewski et al. 2009). The other paternal relatives were identified from these genetically determined patrilineal lines. No female in this sample had sons or nephews of age to be potential mates. Seven females had fathers that were alive during the study period, 2 females had maternal uncles while 3 had paternal uncles, and 5 females had maternal half-brothers while 2 had paternal half-brothers (Table 3.1). The effect of kinship was treated in one of two ways: 1) generally, where we combined all related dyads into a single category (henceforth general kinship) or 2) specifically, in terms of father, maternal and paternal half-siblings, and maternal and paternal uncles (henceforth specific kinship). While we identified paternal brothers and maternal and paternal uncles in order to not categorize them with unrelated males, there were limited data available for them, particularly paternal brothers and uncles for which we had data for only a single male (Table 3.1).

Female Mating Windows

Female have estrus cycles that last approximately 36 days during which they have conspicuous sexual swellings for about 10-12 days, they are receptive to mating, and ovulation occurs (Tutin 1979; Hasegawa & Hiraiwa-Hasegawa 1983; Wallis 1997; Matsumoto-Oda & Oda 1998; Deschner et al. 2003). However, because of the fission-fusion grouping dynamics of chimpanzees, females may not be observed every day of their maximal tumescence. Additionally, females typically have several cycles before conceiving (Gombe: Tutin & McGinnis 1981; Wallis 1997; Mahale: Nishida et al. 1990; Kibale: Knott 2001; Tai: Deschner & Boesch 2007). Consequently, we calculated our behavioral measures (described below) according to mating windows rather than per estrus cycle.

For each female's mating window, we noted the number of previous offspring they had. By definition, nulliparous females had no prior offspring, primiparous females had one previous offspring, and multiparous females had two or more previous offspring. Nulliparous windows were defined to begin on the day of the first observed mating between the female and a male 12 years old or older, and for primiparous and multiparous females, the start of the mating window began on the day of birth of their previous offspring. Because females can have sexual swellings during pregnancy (Goodall 1986; Nishida et al. 1990; Wallis 1997; Deschner & Boesch 2007), mating windows were closed by known conceptions that led to birth. The end of the mating windows was the last day of observed maximal tumescence of the conception swelling

cycle. Conception cycles were identified by back-calculating 229 days, the average duration of gestation (range 208–235 days) (Goodall 1986; Wallis 1997), from the date of birth of the offspring conceived. When a cycle could not be conclusively identified as the conception cycle because two cycles had maximally tumescent days falling within the range of gestation, the second cycle was included in the analysis (and by default, was the endpoint of the mating window). All of the mating windows examined ended with a conception except for three, which were ended by female death, female emigration, or the end of the study period (Table 3.1).

Behavioral Measures

Mating behavior

Either sex can signal their desire to mate in chimpanzees. Females can initiate copulation by approaching a male, crouching down, and presenting her sexual swelling to him, while males exhibit their sexual interest in a female by inspecting her swelling, and by giving a courtship display, in which they have an erect penis and may show one or more additional behaviors to get the female's attention, such as shaking branches, piloerecting, and rocking bipedally (described in Goodall 1986). Because of male courtship displays, sexual behavior is typically quite conspicuous among chimpanzees, in addition to the loud vocalizations that females often make either during copulation or when they refuse mating by screaming and running away. Copulation does not always follow initiation. In addition to refusing to copulate after another's initiation, mating can also fail if a member of the dyad pulls away from the copulation before ejaculation or if

the copulation is interrupted by a third party. Sub-adults, often the females' offspring, will sometimes interfere by physically getting between the copulating pair, and adult males will sometimes interfere with mating as a form of mate guarding (Tutin 1979).

We examined sexual behavior between dyads using several different measures (Table 3.2). We calculated dyadic rates of behavior for each mating window for each female when she was maximally tumescent, using all group composition and interaction data involving the individuals in the dyad regardless of the identity of the focal chimpanzee.

1) *Sexual activity*

We measured the overall level of sexual interest and activity within each dyad as the frequency of mating-related interactions, involving all successful and failed copulations (henceforth total sexual activity) (Table 3.2). Failed copulations occurred when: 1) a chimpanzee failed to respond the other's initiation, 2) a member of the dyad terminated the copulation before ejaculation, or 3) copulations were interrupted by a third party. This measure was calculated as follows:

Total number of sexual events (successful and failed)

Total time male and female observed together

2) *Successful copulation*

Because dyads could have similar levels of mating interest and activity but vary in how often that activity resulted in completed copulations, we also calculated the rate of successful copulation (henceforth copulation success) as follows (Table 3.2):

$$\frac{\text{Total number of successful copulations}}{\text{Total number of dyadic sexual events (successful and failed)}}$$

The failed copulations included in the count of total sexual events for each dyad were restricted to those not caused by interference from a third party so as to only reflect the effect of the pair.

3) *Failure to mate*

When sexual activity did not result in successful copulation, we determined the frequency at which the female was responsible for the failure to successfully copulate (henceforth female failure to mate) (Table 3.2). These rates were restricted to the subset of failed matings that were not caused by interference from a third party, and in which there was a clear individual responsible for the failed mating. The female failure rate was calculated as follows:

$$\frac{\text{Total number of female preventions of copulation}}{\text{Total number of male and female preventions of copulation}}$$

4) *Initiation*

For all sexual events in which a clear initiator of the copulation was recorded, we calculated the rate at which each member of the dyad initiated mating (Table 3.2).

a) For females (henceforth female initiation), this was calculated as:

$$\frac{\text{Total number of times the female presented to the male}}{\text{Total time male and female observed together}}$$

b) For males (henceforth male initiation), this was calculated as:

$$\frac{\text{Total number of times the male inspected or courtship displayed at the female}}{\text{Total time male and female observed together}}$$

5) *Responsiveness*

To measure the responsiveness of males and females to mating solicitations by the opposite sex, we calculated the rate at which female and male initiation resulted in successful copulation (Table 3.2). The calculation of these rates was restricted to the subset of sexual events in which there was a clear initiator (described above).

a) Female responsiveness was calculated as:

$$\frac{\text{Total number of successful copulations after the male's initiation}}{\text{Total number of times the male inspected and courtship displayed at the female}}$$

b) Male responsiveness was calculated as:

$$\frac{\text{Total number of successful copulations after the female presented}}{\text{Total number of times the female presented to the male}}$$

6) *Male interference*

Because males can interfere with the copulations of other dyads, we also calculated the rates of male interference as follows (Table 3.2):

$$\frac{\text{Total number of interruptions by male (B) of female (A) mating with a male (not B)}}{\text{Total time male (B) and female (A) observed together}}$$

Dyadic association

We quantified the association between the males and females on the days the female was observed using a modified version of the Simple Ratio dyadic association index (DAI) for each dyad, calculated as (Table 3.2):

$$\frac{\text{Time male and female observed together}}{\text{Total time female observed}}$$

(Cairns & Schwager 1987). Separate DAIs were calculated both for days when the female was maximally tumescent and for days when she had no observable swelling of the skin of the anogenital area, and regardless of the focal chimpanzee being followed.

Grooming

Dyadic rates of grooming behavior were calculated from follows in which either the male or female of the dyad was the focal chimpanzee (Table 3.2). Separate rates were calculated for days when the female was observed maximally tumescent and for days when she had no observable swelling of the skin of the anogenital area. Dyadic grooming rates were calculated as:

$$\frac{\text{Time male and female groomed together}}{\text{Total time male and female observed together}}$$

Age and Rank

We recorded the male's and female's age as their age at the end of the mating window. All individuals' dates of birth were known minimally to the month and year, with the exception of six adult males whose birth year was estimated. Male linear dominance rank was determined annually between 1983 and 2006, as previously determined by Wroblewski et al. (2009), and then averaged across the years of each mating window. Ranks were then categorized as high (ranks 1-4), medium (ranks 5-8), or

low (ranks 9 and below). For GM's nulliparous mating window, categorical ranks were determined from Goodall (1986).

Statistical Analysis

We used several statistical tests to examine differences according to kinship (Table 3.3). For the DAI and grooming measures, we tested for differences by kinship using general kinship and a Wilcoxon Rank Sum Test to test for differences between the unrelated and related groups. Because males exhibit a preference for older females as mates (Muller et al. 2007), we accounted for any effect of female age by repeating the test within each of the following female age groups: 1) females under 15 years, 2) females 15-20 years, and 3) females over 20 years. The Wilcoxon Rank Sum test was similarly used to test the effect of kinship on the male interference dataset because there was insufficient variation to fit a Generalized Linear Model (GLM).

We used a Poisson GLM for the total sexual activity and male initiation datasets (Table 3.3). To account for repeated measures on the same individual we included a fixed effect for the female and for the male. Additional fixed effects for female age and male age, in years, and male categorical dominance rank (high, medium, and low) were included in the model. We included a fixed effect for the number of the female's previous offspring when we tested the male initiation dataset. This was not included when we tested the total sexual activity dataset to help the model converge, however the number of previous offspring was closely associated with female age, which was included in the

model (Fig. 3.1). For both datasets we tested for an effect of kinship using specific kinship (Table 3.3).

We used a binomial GLM for the copulation success, female responsiveness, and female failure to mate datasets (Table 3.3). For copulation success and female responsiveness we tested for differences by kinship using specific kinship, while for female failure to mate we tested for an effect of kinship using general kinship because the sample sizes were small for the specific kin types. Again, to account for repeated measures on the same individual we included a fixed effect for the female and for the male for the female responsiveness dataset. However these effects were not included for the copulation success or female failure to mate datasets because there were too few observations across the specific kinship categories to fit the individual effects. Additional fixed effects for female age and male age, in years, and male categorical dominance rank were included in the model. We also included a fixed effect for the number of previous offspring when we tested the copulation success and female responsiveness datasets. This was not included when we tested the female failure to mate dataset to help the model converge, however the number of previous offspring was closely associated with female age, which was included (Fig. 3.1).

The GLM models compared the association and interaction rates of females with related adult males to those with unrelated adult males. For each dataset the GLM models were fit twice: once including the effect of kinship and once without. The difference between the fit of the models (and therefore the effect of kinship) was then analyzed

using an F test. When kinship had a significant effect, tests of each specific kinship category were performed using the Tukey-Kramer post hoc group comparison. All tests with P-values ≤ 0.05 were considered significant. We performed all statistical tests with R software (R Development Core Team 2009).

Finally, the female initiation and, accordingly, the male responsiveness datasets were only analyzed descriptively because they could not be tested statistically. Female initiation and its related male responsiveness variable were unsuitable as responses because of the large number of zeros and the small value of the non-zero responses for female initiation (Fig. 3.2).

RESULTS

Mating behavior

Total sexual activity

Females had the highest average total sexual activity rate with fathers (Fig. 3.3). Their rates with fathers, maternal brothers, and paternal uncles were all higher than with unrelated males. Females had lower rates with paternal brothers, and they had no sexual activity with maternal uncles. Kinship had a significant effect on the average total sexual activity rate of females ($F_{5,172} = 3.337$, $P = 0.007$), however no specific kin type was significantly different from unrelated pairs. There were also no differences between the activity rates of the different kin types, although there was a non-significant trend for

maternal brothers and paternal uncles to differ from each other in their activity rates ($P = 0.085$).

There was considerable individual variation among females in their average total sexual activity rates with fathers (Fig. 3.4a) and maternal brothers (Fig. 3.4b) and in comparison to unrelated males. GM had the highest activity rates with both her father and maternal brothers, while DL and SI had no sexual activity with their father and maternal brother, respectively. Females had approximately the same or lower rates of sexual activity with unrelated males than with related males, with the exception of DL with her father and FN and SI with their maternal brothers. Interestingly, for females with multiple mating windows over which their fathers and maternal brothers were present, they showed differences in their activity rates. GM had the highest activity rates with both her father and maternal brothers in her nulliparous mating window, and her rates generally decreased with both kin types in successive mating windows. In contrast, the female GA showed an increase in sexual activity with relatives between her nulliparous and primiparous mating windows, and FN showed both increases and decreases, but not in a consistent direction, in her sexual activity with her father and maternal brothers across her four mating windows.

Copulation success

Females had the lowest average copulation success rate with fathers (Fig. 3.5). Their rates with fathers, maternal brothers, and paternal brothers were all lower than with

unrelated males while they had higher rates with paternal uncles. Kinship had a significant effect on the copulation success rates of females ($F_{4,153} = 4.394$, $P = 0.002$; Fig. 3.5; Fig. 3.6). Successful copulation rates were significantly lower with maternal brothers than with unrelated males ($P = 0.007$), and there was a non-significant trend for fathers and daughters to have lower rates than unrelated dyads ($P = 0.098$). Similarly, both maternal brothers and fathers had lower rates than paternal uncles, significantly different ($P = 0.017$) and a trend of significance respectively ($P = 0.054$). No other kin type had copulation success rates that were different than unrelated dyads or each other.

Females also showed considerable variation in their average copulation success rates with fathers (Fig. 3.7a) and maternal brothers (Fig. 3.7b) and in comparison to unrelated males. FS, GA, and GM showed little avoidance of their relatives as they nearly always had successful copulation for each sexual event they were engaged in with their fathers and maternal brothers. They also had approximately the same or lower rates of success with unrelated males than with related males. In contrast, SI and TG had more intermediate copulation success rates with related males, while FN nearly always avoided her relatives, but they all had lower success rates with fathers than with unrelated males. FN also had considerably lower success rates with her maternal brothers than unrelated males, but TG had little difference. For females with multiple mating windows over which their fathers and maternal brothers were present, they showed differences in their copulation success rates both within and between females.

Female failure to mate

Females were responsible for the vast majority (80% or more) of the failures to mate with males, with the exception of with their paternal brothers (Fig. 3.8). Females failed to mate most frequently with fathers, while their rates with maternal brothers and paternal uncles were higher than with unrelated males. Failure rates with paternal brothers were lower than with unrelated males. Nonetheless, kinship was not a significant predictor of the average female failure rate ($F_{1,59} = 0.025$, $P = 0.875$).

Initiation

1) Female

Females had the lowest average initiation rate with fathers, while rates with maternal and paternal brothers, and paternal uncles were higher than with unrelated males (Fig. 3.9). However, female initiation rates could not be modeled because of the zero-heavy nature of the data (Fig. 3.2).

2) Male

Males were responsible for the majority of initiations between dyads (Fig. 3.10a). Fathers had the highest initiation rate with females (Fig. 3.10b), while maternal brothers and paternal uncles also initiated more frequently with females than unrelated males. Kinship was not a significant predictor of the average male initiation rate ($F_{5,171} = 0.971$, $P = 0.437$).

Responsiveness

1) Female

Females had the lowest average responsiveness rate to male initiation with fathers, while rates with maternal and paternal brothers, and paternal uncles were higher than with unrelated males (Fig. 3.11). Kinship was not a significant predictor of the average female responsiveness rate ($F_{3,62} = 0.844$, $P = 0.475$).

2) Male

Paternal brothers had the lowest average responsiveness rate to female initiation, while rates of fathers and maternal brothers, and paternal uncles were higher than those of unrelated males (Fig. 3.12). However, male responsiveness rates could not be modeled because of the zero-heavy nature of the data.

Male interference

All kin types tested had lower average male interference rates of female copulations than unrelated males. When the interference rates of related males were compared to those of unrelated males, the difference was not significant for any female age group (young: $W = 571$, $N = 76$, $P = 0.45$; middle: $W = 622$, $N = 94$, $P = 0.247$; old: $W = 139$, $N = 39$, $P = 0.841$; Fig. 3.13).

DAI

Females generally increased their association with all adult males, whether the males were related or unrelated, when they were maximally tumescent compared to when they were not tumescent during the mating windows (Fig. 3.14). Substantial increases occurred with unrelated males, fathers, maternal brothers, and paternal uncles, and less so paternal brothers and maternal uncles. When the DAI of maximally tumescent females with related males was compared to that with unrelated males, the difference was not significant for any female age group (young: $W = 585$, $N = 80$, $P = 0.872$; middle: $W = 969.5$, $N = 97$, $P = 0.569$; old: $W = 185.5$, $N = 43$, $P = 0.812$; Fig. 3.14; Fig. 3.15).

Grooming

Females substantially decreased their total grooming rate with maternal brothers when maximally tumescent compared to when they were not tumescent (Fig. 3.16). They showed slight decreases in grooming rates with fathers and paternal brothers, and slight increases in grooming rates with unrelated males and paternal uncles. When the total grooming rates of maximally tumescent females with related males was compared to that with unrelated males, the difference was not significant for any female age group (young: $W = 400$, $N = 59$, $P = 0.256$; middle: $W = 636$, $N = 77$, $P = 0.761$; old: $W = 172$, $N = 37$, $P = 0.189$; Fig. 3.16; Fig. 3.17).

DISCUSSION

In this study, we present the first evidence suggesting female chimpanzees avoid mating with their fathers. There was a trend of reduced successful copulation between fathers and daughters compared with unrelated dyads. In addition we found significantly reduced successful copulation between maternal siblings compared with unrelated dyads, which supports previous findings (Pusey 1980; Goodall 1986; Constable et al. 2001; Pusey 2005). Interestingly, there were no significant differences in total sexual activity between related and unrelated dyads. These patterns for successful copulation and sexual activity are similar to those found in baboons, in which paternal siblings were not less likely to form sexual consorts, but their consorts were significantly less cohesive in affiliative and sexual behavior (Alberts 1999). Given the small amount of data available for paternal brothers and maternal and paternal uncles, we will limit our discussion to fathers and maternal brothers.

While the differences were not significant, the other behavioral patterns were also suggestive of mating avoidance. Fathers and maternal brothers exhibited lower rates of interference in related females' copulations with other males, suggesting that they did not compete as hard as other males over their female relatives as mates. In addition, females had lower rates of initiation and responsiveness with their fathers than with unrelated males, but surprisingly not fathers with their daughters, and females failed to mate more with their fathers and maternal brothers, as we would predict if they were avoiding kin as mates.

Neither the grooming or association patterns conformed to our prediction of decreased affiliative behavior amongst relatives when females are maximally tumescent. Females are typically more gregarious when they are maximally tumescent (Goodall 1986; Pepper et al. 1999; Matsumoto-Oda 2002), and theoretically the fission-fusion grouping patterns of chimpanzees provide females the opportunity to choose whether to associate with particular males (Nishida 1968; Goodall 1986; Boesch & Boesch-Achermann 2000). We also observed an increase in female gregariousness as they increased their association with all males when they were sexually receptive compared to when they were not, but the lack of a significant difference in females' DAI with related compared to unrelated males when maximally tumescent indicates that females do not avoid associating with kin as a means to avoid inbreeding with them. In practice it may be difficult for females to avoid particular males because males are attracted to parties by the presence estrus females, and the number of males in a party increases with the presence of swelling females (Matsumoto-Oda 1999b). Although we did not have the necessary data to test this, it will be interesting to explore female spatial proximity patterns within social parties to see whether related dyads spend more time at greater distances from each other within groups as an alternative means of avoiding kin, but the fact that grooming rates did not differ between related and unrelated dyads indicates that spatial proximity may not be affected either.

When taken together, the pattern of increased total sexual activity as well as increased male, but not female, initiation suggests that it is primarily the males' effort that leads to the sexual activity between relatives. Furthermore, females were responsible

for a vast majority of the failures to mate amongst related dyads and had higher rates of female-caused failures with both fathers and maternal brothers. This suggests that it is the females that are choosier and the ones primarily responsible for the lower successful copulation rates and mating avoidance with relatives. Similarly, female baboons were also found to avoid mating more than males (Packer 1979). With females' investment in eggs, and more limited potential for reproduction given their extensive investment in gestation, lactation and parental care offspring, we would expect females to be more resistant to mating as the costs of inbreeding are likely higher for them than for males (Darwin 1871; Orians 1969; Trivers 1972; Emlen & Oring 1977).

However, it is clear that mating avoidance is not universal amongst females. There was considerable variation among females in their mating behavior with close relatives, as has been observed previously (Pusey 1980; Goodall 1986; Constable et al. 2001; Pusey 2005; Stumpf et al. 2009). The female, GM, who showed the least avoidance of her father and maternal brothers overall, was noted by Goodall (1986) to be unusual in her lack of avoidance of relatives. Interestingly, GM showed the most sexual activity with them in her nulliparous mating window, and showed a decrease in sexual activity with relatives in successive windows. Thus, it is possible that females show less avoidance in their nulliparous mating window when there is a period of months to years in which they have sexual swellings but are still not fertile (Tutin 1979; Goodall 1986; Pusey 1990). While we attempted to account for this period of adolescent sterility by only starting the mating window after the females' first observed mating with an older male (≥ 12 year old), whose interest is generally considered to be an indicator of female sexual

maturity, given that half of our data for fathers and daughters consisted of nulliparous mating windows, compared to only 30% for maternal siblings (Fig. 3.4a), we may expect to see a stronger effect with fathers as more data becomes available for primi- and multiparous mating windows.

Given the behavioral bias found between daughters and fathers in this study, an important question to ask is, what mechanism could daughters use to recognize their fathers to avoid inbreeding in a non-monogamous species with no obvious paternal care such as chimpanzees? Several possible mechanisms could be used, and none are mutually exclusive (Sherman et al. 1997; Widdig 2007). Fathers and offspring were previously thought not to have the social familiarity that mothers and offspring and maternal siblings have through their obvious and lengthy association (Goodall 1986; Silk 2002; Rendall 2004; Strier 2004; Widdig 2007), but the differential behavior now reported between fathers and their infants and the infants' mothers (Lehmann et al. 2006) could be a means through which offspring, and particularly females, gain familiarity with their fathers. Chimpanzees may also employ phenotype-matching mechanisms to recognize paternal relatives, whereby a physical trait varies closely with the degree of relatedness. Face recognition tests of captive chimpanzees showed that they can detect visual similarity between both maternal and paternal parent-offspring pairs (Parr & de Waal 1999; Parr et al. in press). For paternal kin, and particularly fathers and offspring, a self-referent phenotype matching mechanism may be the most reliable, by which an individual could compare the traits of others to its own, rather than to those of other close paternal relatives with whom they may not be familiar. A scent-based cue may be one such

mechanism, and a strong candidate is the odor correlated with the major histocompatibility complex (MHC), the set of genes coding for antigen-presenting proteins in the immune system. Indeed, humans and other animals make olfactory distinctions that correlate with fine differences in MHC genotype (humans: Wedekind et al. 1995; Jacob et al. 2002; reviewed in Loisel et al. 2008). Similarly, genital olfactory cues of lemurs, *Lemur catta*, signal their individual genetic diversity, and the genetic relatedness of individuals correlates with their olfactory chemical distance (Charpentier et al. 2008b). In addition, the odor profiles of relatives most overlap during their breeding season, suggesting that the cue is important for recognizing relatives in order to avoid inbreeding (Boulet et al. 2009).

Familiarity through a shared association with their mother has been implicated as a strong and important recognition mechanism among maternal siblings (Goodall 1986; Rendall 2004). While they had significantly fewer successful copulations than unrelated dyads, surprisingly their total sexual activity was not different than unrelated dyads, and mating avoidance of maternal brothers was quite variable amongst females. This variability in avoidance is consistent with other studies where mating amongst adult maternal siblings ranged from being rarely observed (Pusey 1980; Goodall 1986; Pusey 2005) to occurring at high rates or rates not different than with other males (Pusey 2005; Stumpf et al. 2009). However, it is important to note that although females mate with relatives such as fathers and maternal brothers, they have not conceived with them. There is no documented conception between father and daughter or maternal siblings, and only one inbred offspring has ever occurred between a mother and son, across study sites

(Gombe: Constable et al. 2001; Wroblewski et al. 2009; Bossou (Guinea): Sugiyama et al. 1993; Tai Forest (Cote d'Ivoire): Vigilant et al. 2001; Boesch et al. 2006; Budongo (Uganda): Reynolds 2005; Mahale (Tanzania): Inoue et al. 2008). With more detailed data and increased sample size, it will be important to compare mating behavior between conceptive and non-conceptive cycles, and on the days of the periovulatory period (POP) within cycles to non-POP days. Females were found to be less promiscuous during the POP but more so outside the POP (Stumpf & Boesch 2005, 2006), and so it may be that females are able to avoid inbreeding by only mating with relatives outside the most likely time of conception. Furthermore, as more data accumulate, it will be important to determine if natal females are more likely to go off alone with unrelated males on sexual consortships than immigrant females, particularly during their conceptive cycles, as a means of avoiding their male relatives in the community, as suggested by Constable et al. (2001).

While this study suggests that daughters can recognize and avoid mating with their fathers, why then do we not see differential behavior amongst fathers and sons (Chapter 2)? Female promiscuity may effectively confuse paternity for males (Trivers 1972; Hrdy 1974; Clutton-Brock 1991), and differences in recognition capabilities and mechanisms may enable daughters but not sons to recognize their fathers. Such bias towards opposite sex recognition was observed in captive chimpanzee facial similarity tests, where chimpanzees were significantly better at matching opposite sex parent-offspring pairs than same sex parent-offspring pairs (Parr and de Waal 1999; Parr et al. in press). However, if we assume that fathers are able to recognize both their male and

female infant offspring, as suggested by Lehmann et al. 2006, then presumably the ability is not lost with the increasing age of the offspring. That would then suggest that the costs of inbreeding are not sufficiently high for males to warrant differential behavior by fathers, nor are the benefits of fathers helping their juvenile and adolescent sons.

While females usually disperse at sexual maturity in chimpanzees, the extent to which they do so is variable across study sites (Gombe: Pusey et al. 1997; Tai: Boesch & Boesch-Achermann 2000; Mahale: Nishida et al. 2003; Kibale: Kahlenberg et al. 2008a). Inbreeding avoidance may be an influential factor in the evolution of female-biased dispersal in chimpanzees, however Stumpf et al. (2009) showed it does not appear to be a proximate explanation of females' decision to disperse. Regardless of the reason females emigrate, when they choose to stay in their natal community they face the risk of mating and inbreeding with close relatives such as fathers, sons, brothers and uncles. Our new evidence suggesting that daughters recognize and avoid fathers as mates, in addition to maternal kin, means that females that do not disperse can avoid the costs of inbreeding as well as the costs of dispersal, such as aggression (Kahlenberg et al. 2008b; Pusey et al. 2008b), while maximizing the benefits of their affiliative relationships and territorial knowledge of food resources within their natal community (Pusey et al. 1997; Williams et al. 2002a; Murray et al. 2007; Gilby & Wrangham 2008; Langergraber et al. 2009; Silk et al. 2009).

CONCLUSIONS

This study suggests that there is paternal kin discrimination and mating avoidance of fathers by daughters and is the first suggestion of paternal kin discrimination of fathers by non-infant offspring in chimpanzees. However, our study shows that females do not completely avoid mating with their fathers and maternal brothers. Nonetheless they manage to avoid inbreeding as no inbred offspring have been sired between them (Chapter 1). Future studies need to investigate the timing of mating between relatives because females may allow copulations with their relatives when they are less likely to conceive as a possible means of inbreeding avoidance. This study also provides further evidence that paternal kin discrimination is socioecologically contextual in chimpanzees. Other studies have shown that fathers may have some preference for their infant offspring but that paternal siblings have no apparent preference for each other. In contrast, we did not find evidence that fathers can recognize their male or female offspring. Our preliminary study (Chapter 2) showed that fathers do not have behavioral bias in association or interactions with their juvenile and adolescent sons, nor in this study in their mating behavior with daughters. However, this study suggests that daughters can recognize their fathers because of their bias against mating with their fathers. Thus, future studies also need to test these apparent sex differences in kin recognition ability. Determining whether males cannot recognize their offspring, or recognize their offspring but do not bias behavior towards them, will more clearly determine whether promiscuity obscures paternity for males. Elucidating the recognition mechanisms as well as the costs

and benefits to recognition and behavioral bias are essential to understanding the conditions under which paternal kin discrimination evolves.

FIGURE CAPTIONS

Figure 3. 1.: Number of previous offspring by female age for each mating window.

Figure 3. 2.: Distribution of the counts of female initiation by dyadic mating window.

Figure 3. 3.: The average total sexual activity rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type (e.g. GB-FN nulliparous). Error bars indicate ± 1 SE.

Figure 3. 4.: Individual variation in females' average total sexual activity rate with a) fathers, and b) maternal brothers, both across all mating windows and compared to unrelated males (Female) and by individual mating window with the related male (Female mating window). Female mating windows are represented by the females' ID code and their number of previous offspring (e.g. FN's nulliparous mating window is represented by FN0). Error bars for Female graphs indicate ± 1 SE.

Figure 3. 5.: The average copulation success rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

** Statistically significant difference from unrelated dyads ($P \leq 0.05$).

* Non-significant trend of a difference from unrelated dyads ($P \leq 0.1$).

Figure 3. 6.: The Generalized Linear Model fit average of the copulation success rate for each kin type after accounting for the fixed effects for female and male age, in years, male categorical dominance rank, and number of previous offspring. Maternal uncles are not represented because females did not have any sexual activity with them. Error bars indicate ± 1 SD.

** Statistically significant difference from unrelated dyads ($P \leq 0.05$).

* Non-significant trend of a difference from unrelated dyads ($P \leq 0.1$).

Figure 3. 7.: Individual variation in females' average copulation success rate with a) fathers, and b) maternal brothers, both across all mating windows and compared to unrelated males (Female) and by individual mating window with the related male (Female mating window). Mating windows are represented by the females' ID code and their number of previous offspring (e.g. FN's nulliparous mating window is represented by FN0). NA means not applicable (females did not have any sexual activity with that kin type). Error bars for Female graphs indicate ± 1 SE.

Figure 3. 8.: The average female failure rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 9.: The average female initiation rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 10.: a) The male proportion of total dyadic initiation, and b) the average male initiation rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 11.: The average female responsiveness rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 12.: The average male responsiveness rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 13.: The average male interference rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA

means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 14.: The average DAI for each kin type for both maximally tumescent days (i.e. sexually receptive) within mating windows and non-tumescent days within mating windows. Numbers are the number of unique male-female mating window data points available per kin type. Error bars indicate ± 1 SE.

Figure 3. 15.: Boxplot of the DAIs for related and unrelated dyads during mating windows.

Figure 3. 16.: The average total grooming rate for each kin type for both maximally tumescent days (i.e. sexually receptive) within mating windows and non-tumescent days within mating windows. Numbers are the number of unique male-female mating window data points available per kin type. Error bars indicate ± 1 SE.

Figure 3. 17.: Boxplot of the total grooming rates for related and unrelated dyads during mating windows.

Table 3. 1. Data available for each female and related males per mating window

Female	# Previous offspring	Window start date	Window stop date	Father	Maternal Brother	Paternal Brother	Maternal Uncle	Paternal Uncle
DL	0	4/27/2000	8/18/2002	BE				
	1	4/4/2003	4/26/2005					
FN	0	9/8/1989	9/28/1991	GB	FD, FR			GL
	1	4/29/1992	4/24/1996	GB	FD, FR			GL
	2	12/9/1996	10/26/1999	GB	FD, FR			GL
	3	5/27/2000	9/9/2003	GB	FD, FR, FO			GL
FS	0	1/6/1995	1/16/1996 [#]	GB	FD, FR			GL
GA	0	12/15/2003	9/23/2005	WL		FO	GB, GL	
	1	4/28/2006	10/9/2006	WL		FO	GL	
GM	0	12/20/1980	10/7/1981	EV	GB			
	1	5/21/1982	10/12/1986	EV	GB			
	2	5/15/1987	8/28/1987	EV	GB			
	3	4/5/1988	7/9/1992	EV	GB, GL			
	4	2/14/1993	12/26/1997		GB, GL			
	5	7/13/1998	6/6/2003		GB, GL			
SI	0	10/15/2003	12/31/2006 [†]	WL	SL	FO		
SR	0	10/16/2003	1/3/2004 [*]	(BE)			SL	
	1	8/25/2004	11/5/2006	(BE)			SL	
TG	0	12/22/1998	8/11/2000	GB				GL
	1	3/7/2001	2/10/2006		TN			GL

[†] SI did not conceive before the end of the study period.

^{*} SR died before conceiving.

[#] FS emigrated before conceiving.

() Paternity was known for SR, however her father died before she reached sexual maturity.

Table 3. 2. Summary of behavioral measures

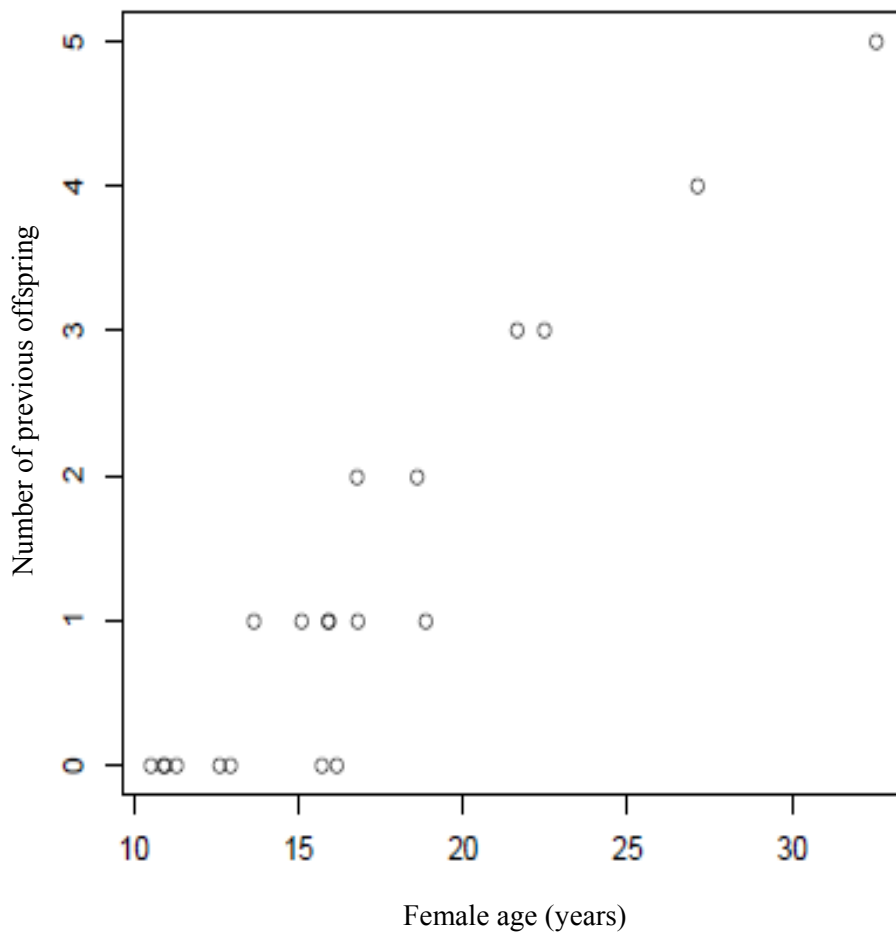
Measure	Calculation	Data source	Tumescence
Total sexual activity	Sexual events (successful and failed)/Dyadic time together	All available	Maximal
Copulation success	Successful copulations/ Sexual events (successful and failed)	All available	Maximal
Female failure to mate	Female copulation preventions/ Total preventions (male and female)	All available	Maximal
Initiation	a. Female: initiations/ Dyadic time together b. Male: initiations/ Dyadic time together	All available	Maximal
Responsiveness	a. Female: copulations/ Male initiations b. Male: copulations/ Female initiations	All available	Maximal
Male interference	Male interference/ Dyadic time together	All available	Maximal
DAI	Dyadic time together/ Total time female observed	All available	Maximal and non-maximal
Grooming	Time spent grooming together/ Dyadic time together	Focal only	Maximal and non-maximal

Table 3. 3. Summary of statistical tests used for each measure

	Statistical test	Kinship	Fixed effects			Individual effects		
			# Previous offspring	Female age	Male age	Male rank	Female	Male
Total sexual activity	Poisson GLM	Specific		X	X	X	X	X
Copulation success	Binomial GLM	Specific	X	X	X	X		
Female initiation	NA							
Male initiation	Poisson GLM	Specific	X	X	X	X	X	X
Female responsiveness	Binomial GLM	Specific	X	X	X	X	X	X
Male responsiveness	NA							
Female failure to mate	Binomial GLM	General		X	X	X		
Male interference	Wilcoxon Rank Sum	General		X-Categorical				
DAI	Wilcoxon Rank Sum	General		X-Categorical				
Total grooming	Wilcoxon Rank Sum	General		X-Categorical				

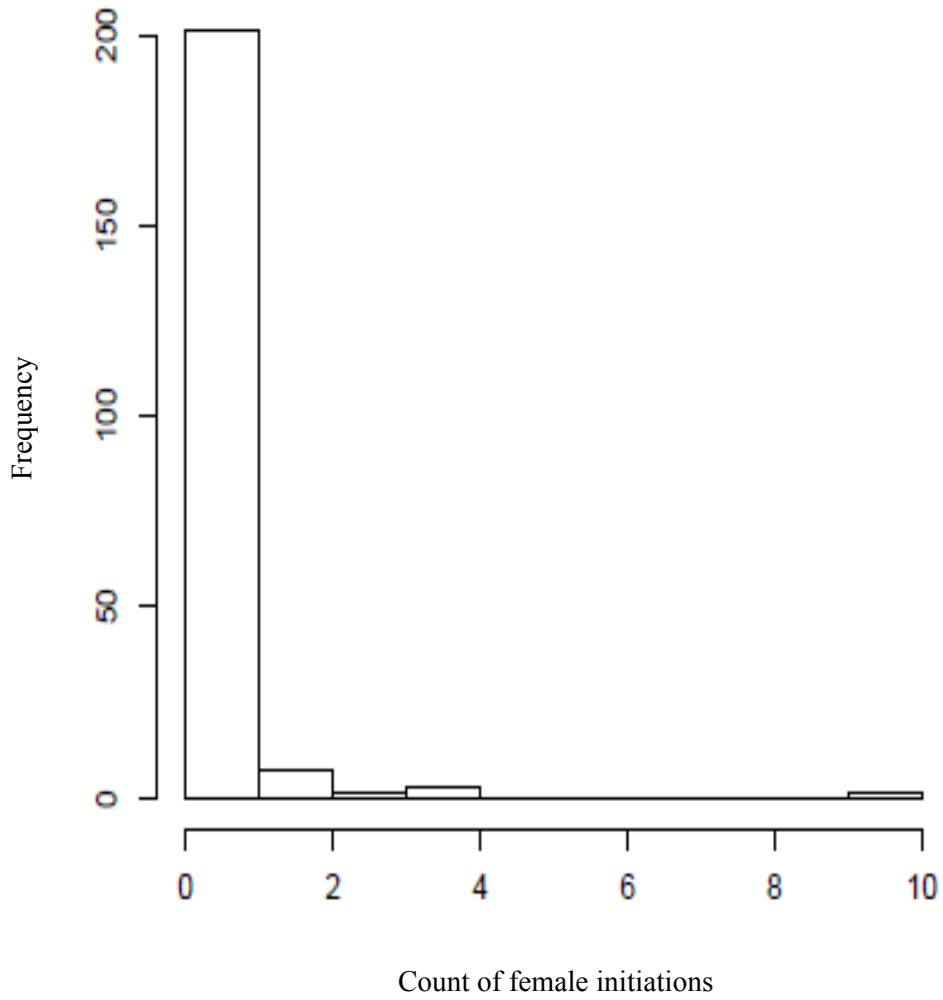
GLM is a Generalized Linear Model. NA means that the measure could not be tested with the data available. The effect of kinship was tested in two ways: either generally (General) in the categories related and unrelated, or specifically (Specific), in terms of father, maternal and paternal half-siblings, and maternal and paternal uncles. X designates that the effect was included in the model. Female age for the Wilcoxon Rank Sum Tests was accounted for by repeating the test across female age groups (Categorical). When included, individual effects were included as a fixed effect.

Figure 3. 1. Number of females' previous offspring by female age



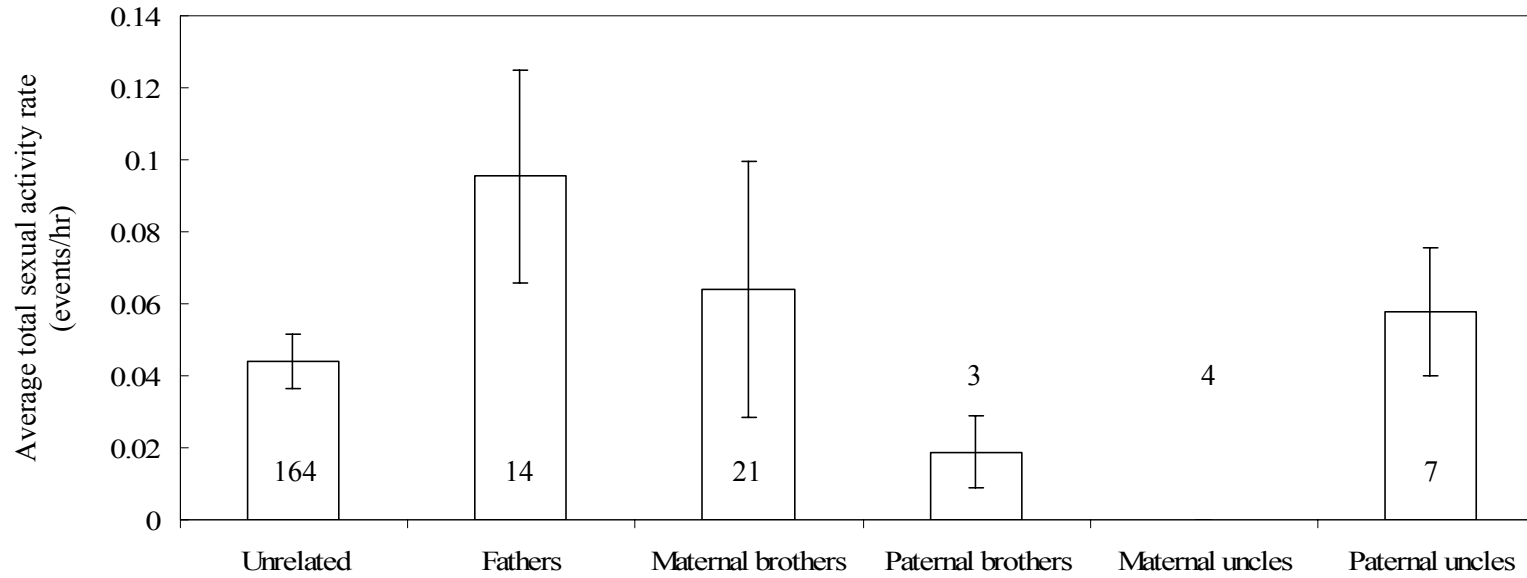
Number of previous offspring by female age for each mating window.

Figure 3. 2. Histogram of the count of female initiations



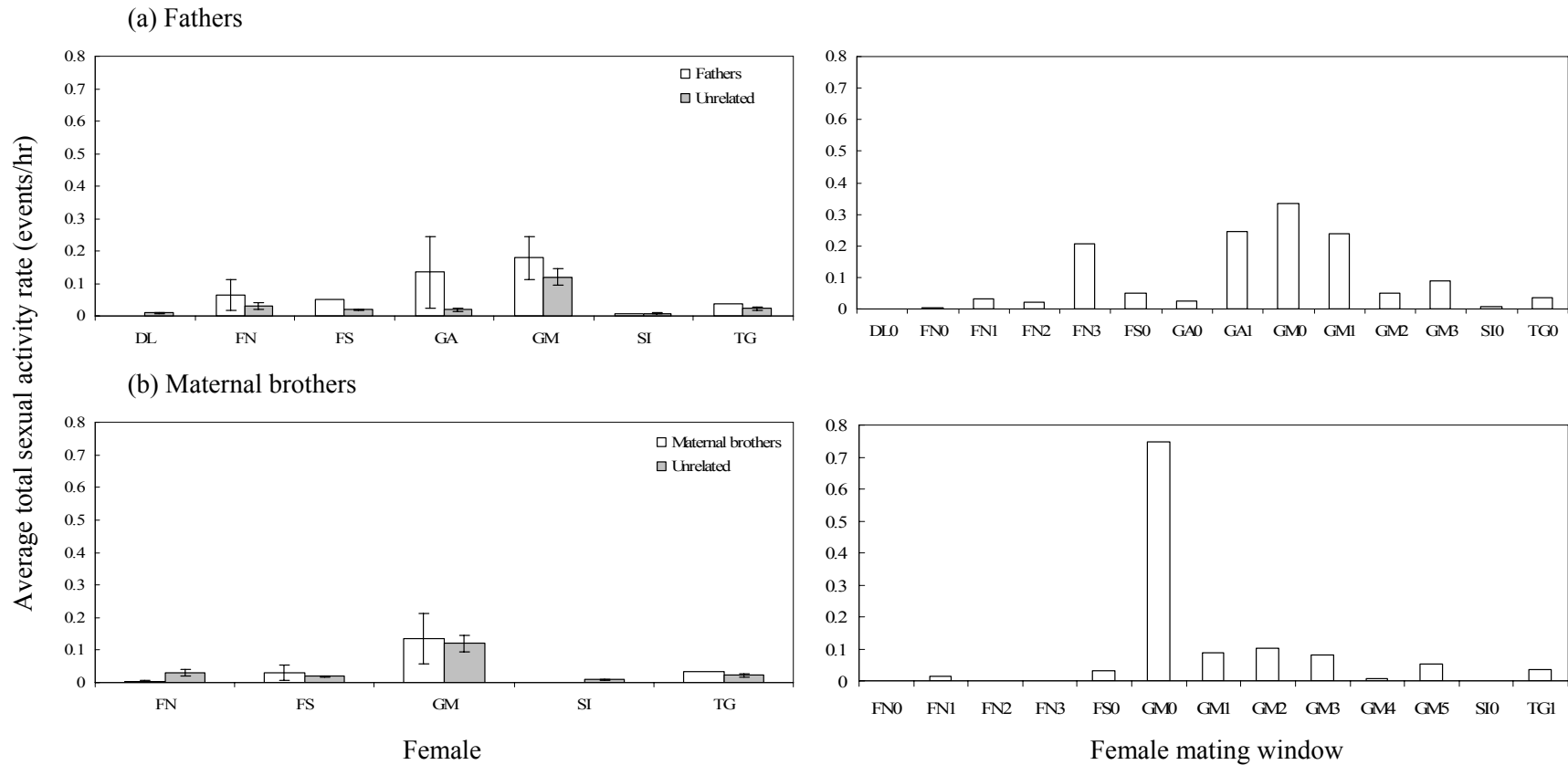
Distribution of the counts of female initiation by dyadic mating window.

Figure 3. 3. Sexual activity by kin type



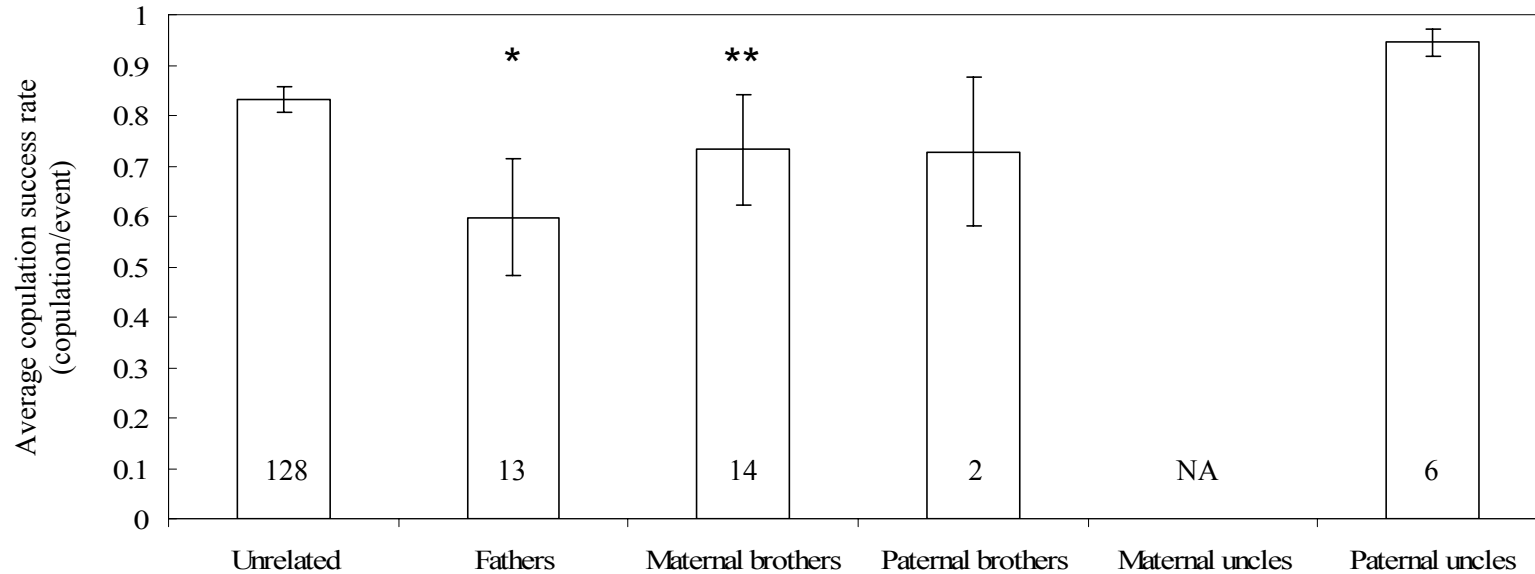
The average total sexual activity rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type (e.g. GB-FN nulliparous). Error bars indicate ± 1 SE.

Figure 3. 4. Individual female sexual activity with fathers and maternal brothers



Individual variation in females' average total sexual activity rate with a) fathers, and b) maternal brothers, both across all mating windows and compared to unrelated males (Female) and by individual mating window with the related male (Female mating window). Female mating windows are represented by the females' ID code and their number of previous offspring (e.g. FN's nulliparous mating window is represented by FN0). Error bars for Female graphs indicate ± 1 SE.

Figure 3. 5. Copulation success by kin type

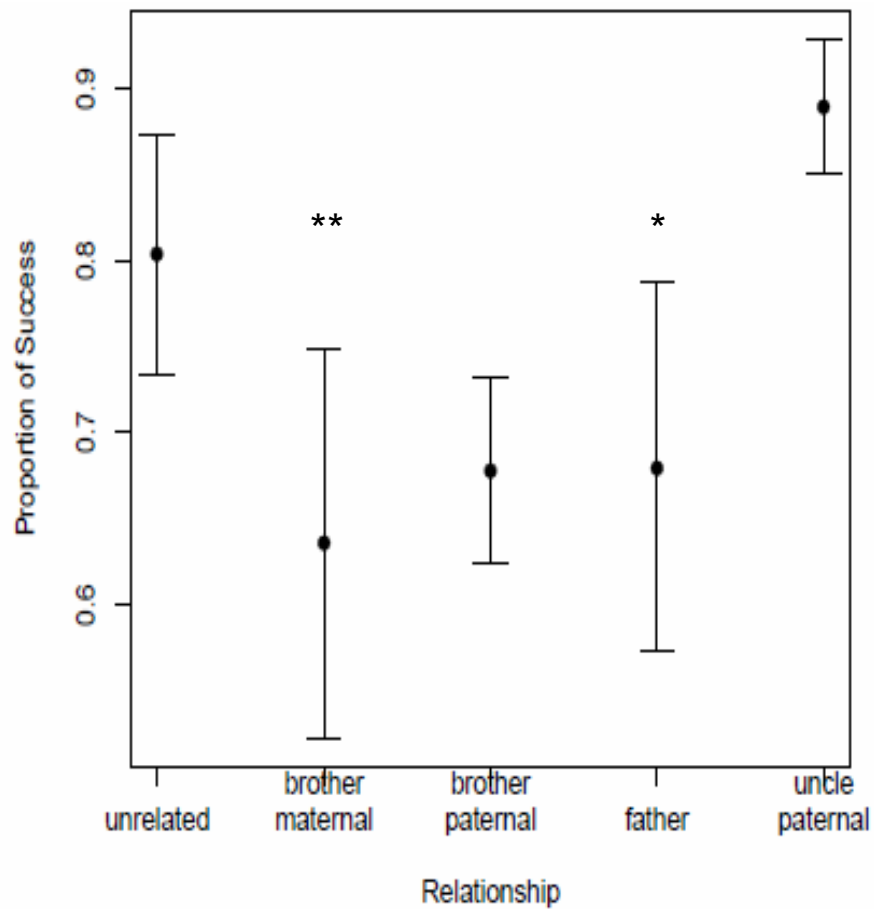


The average copulation success rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

** Statistically significant difference from unrelated dyads ($P \leq 0.05$).

* Non-significant trend of a difference from unrelated dyads ($P \leq 0.1$).

Figure 3. 6. GLM fit rate of copulation success by kin type

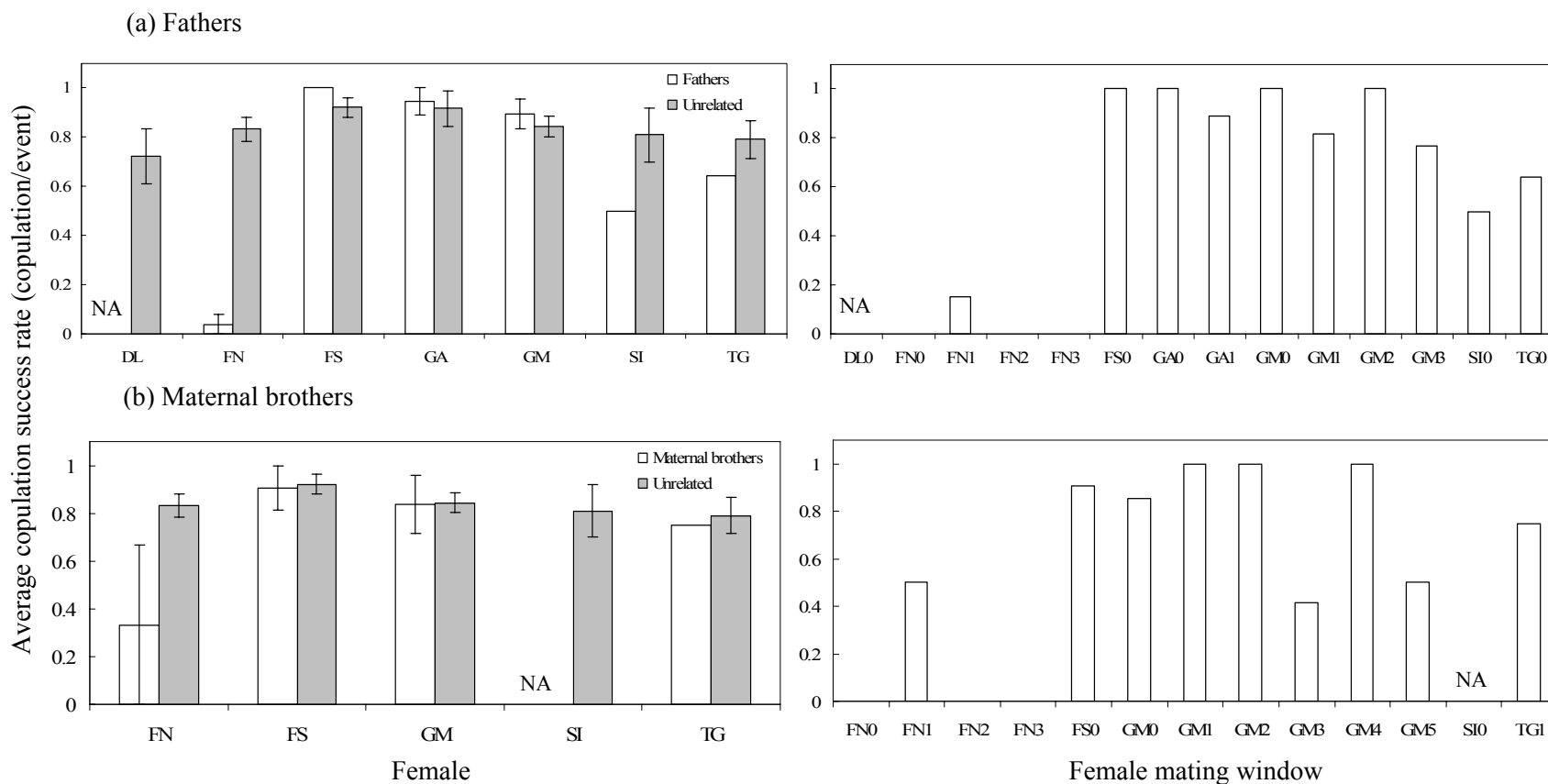


The Generalized Linear Model fit average of the copulation success rate for each kin type after accounting for the fixed effects for female and male age, in years, male categorical dominance rank, and number of previous offspring. Maternal uncles are not represented because females did not have any sexual activity with them. Error bars indicate ± 1 SD.

** Statistically significant difference from unrelated dyads ($P \leq 0.05$).

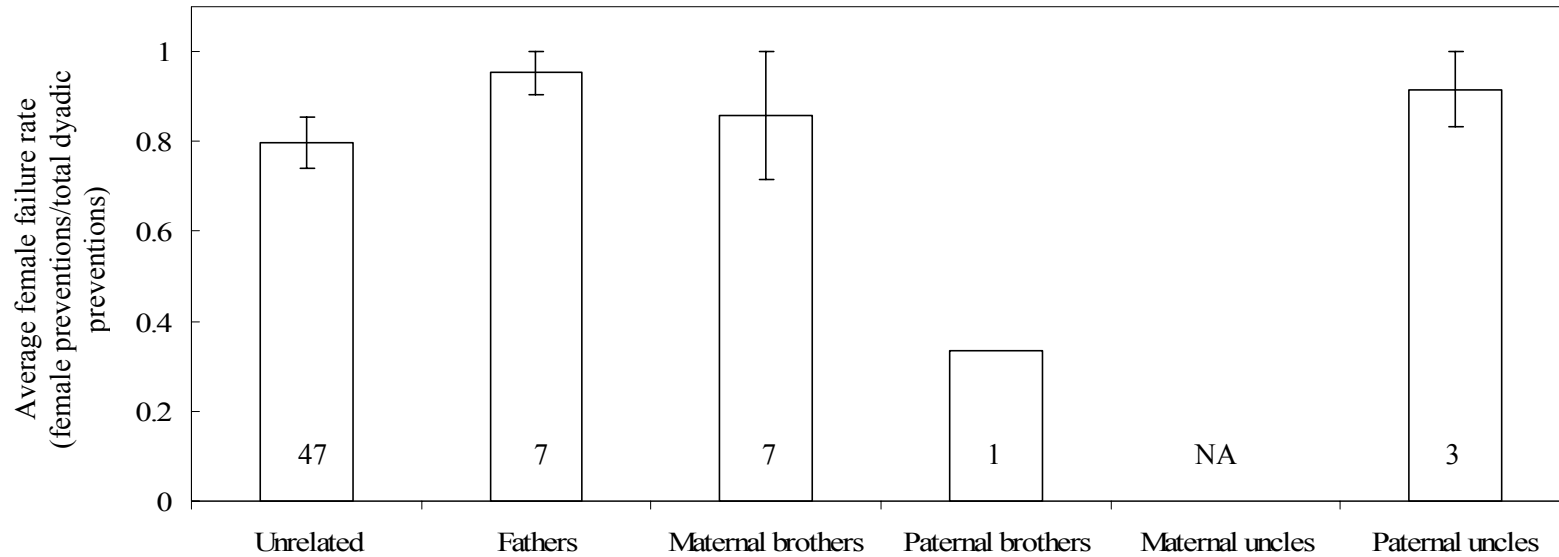
* Non-significant trend of a difference from unrelated dyads ($P \leq 0.1$).

Figure 3. 7. Individual female copulation success with fathers and maternal brothers



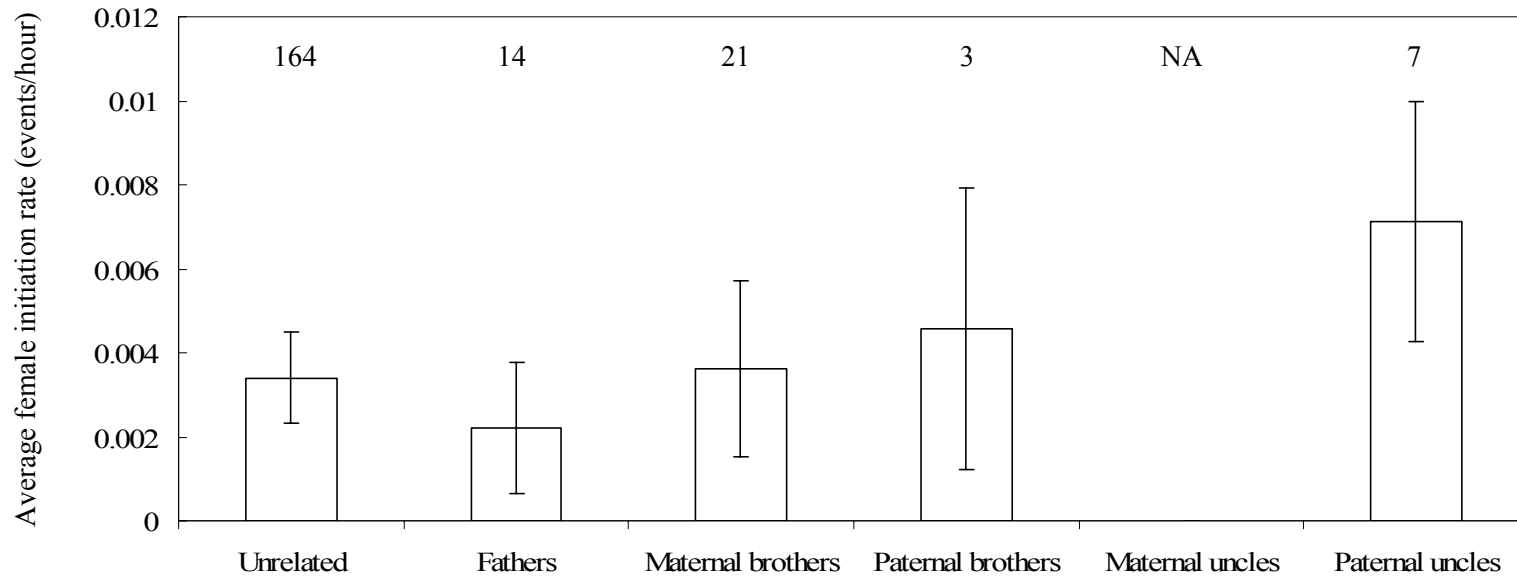
Individual variation in females' average copulation success rate with a) fathers, and b) maternal brothers, both across all mating windows and compared to unrelated males (Female) and by individual mating window with the related male (Female mating window). Mating windows are represented by the females' ID code and their number of previous offspring (e.g. FN's nulliparous mating window is represented by FN0). NA means not applicable (females did not have any sexual activity with that kin type). Error bars for Female graphs indicate ± 1 SE.

Figure 3. 8. Female failure to mate by kin type



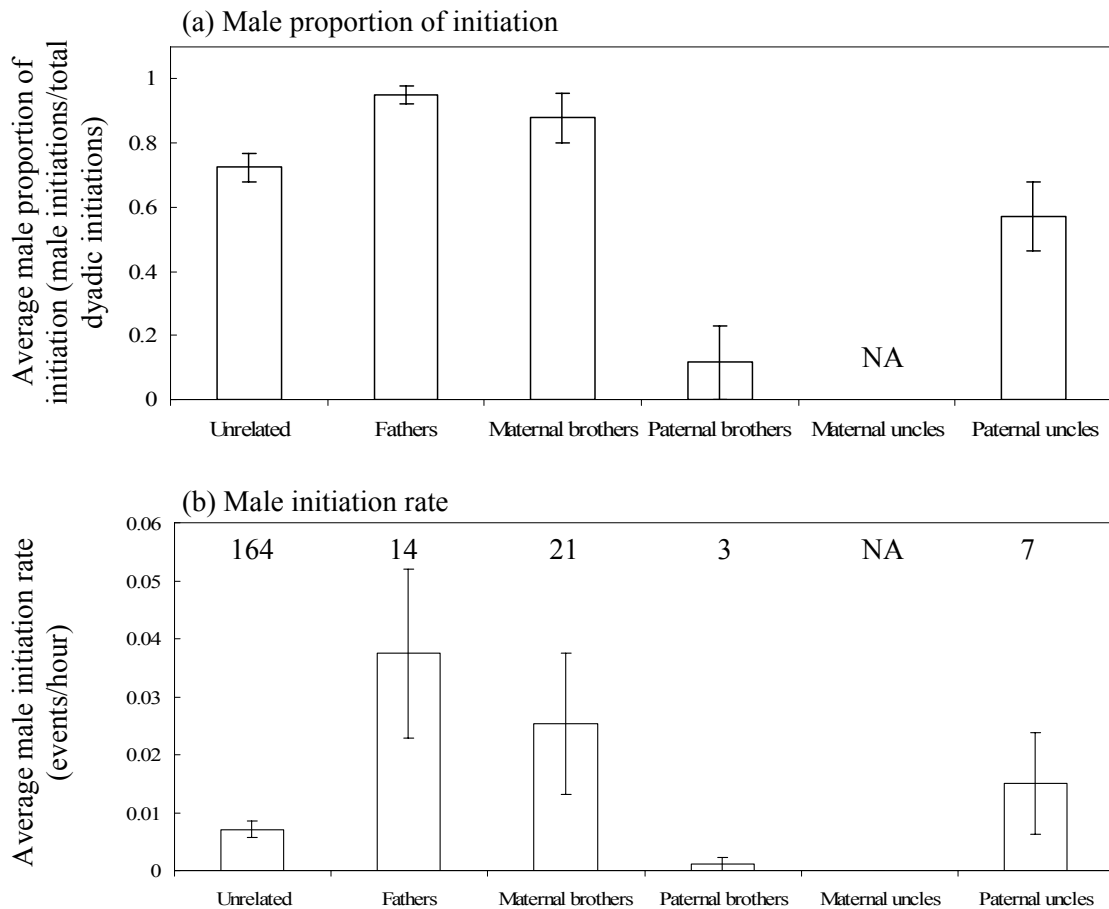
The average female failure rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 9. Female initiation by kin type



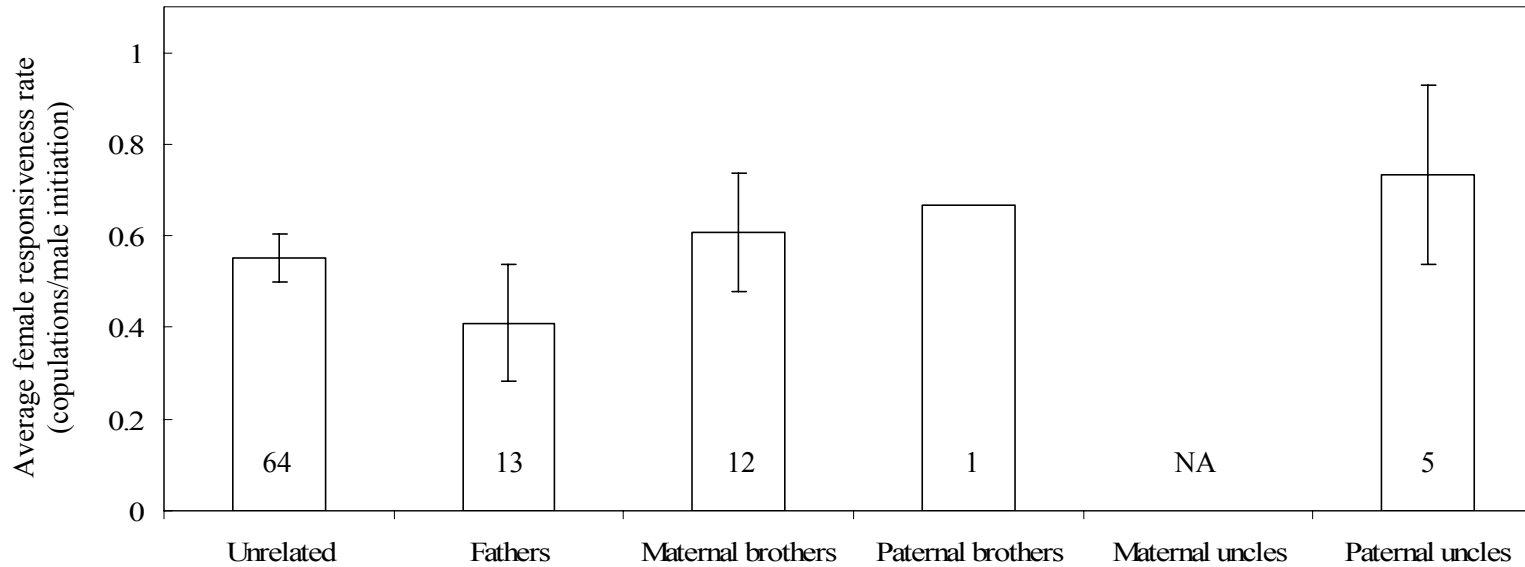
The average female initiation rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 10. Male initiation by kin type



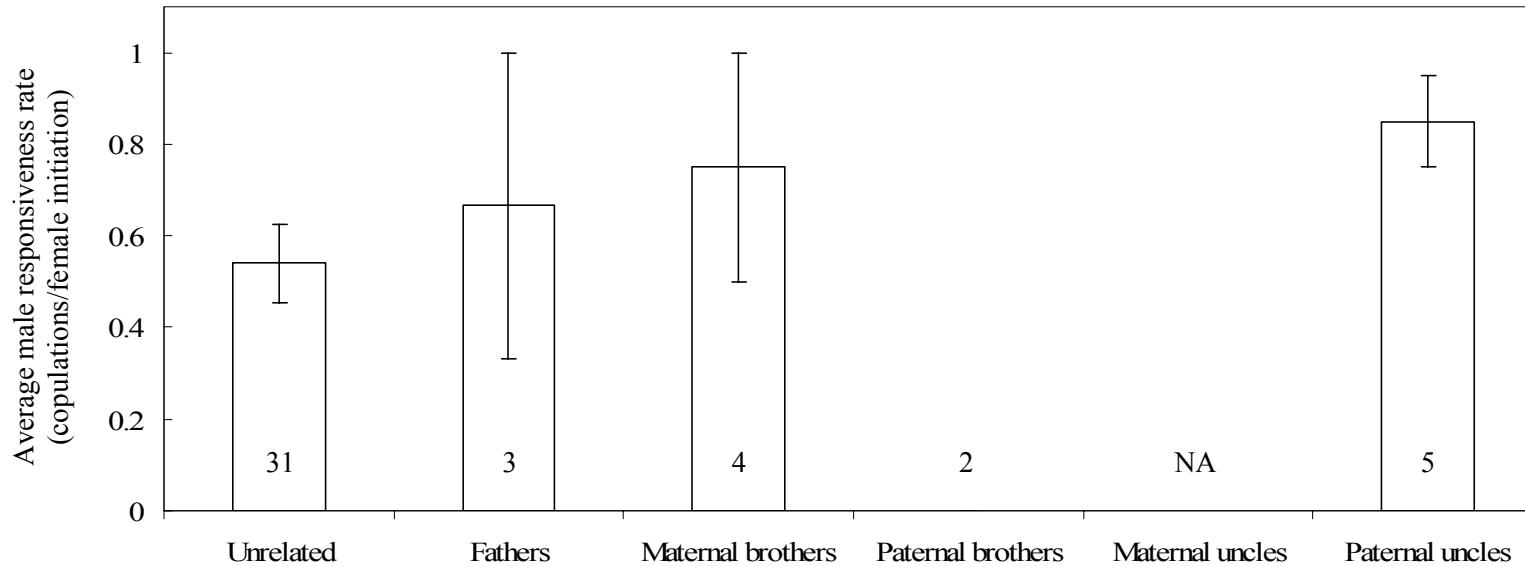
a) The male proportion of total dyadic initiation, and b) the average male initiation rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 11. Female responsiveness by kin type



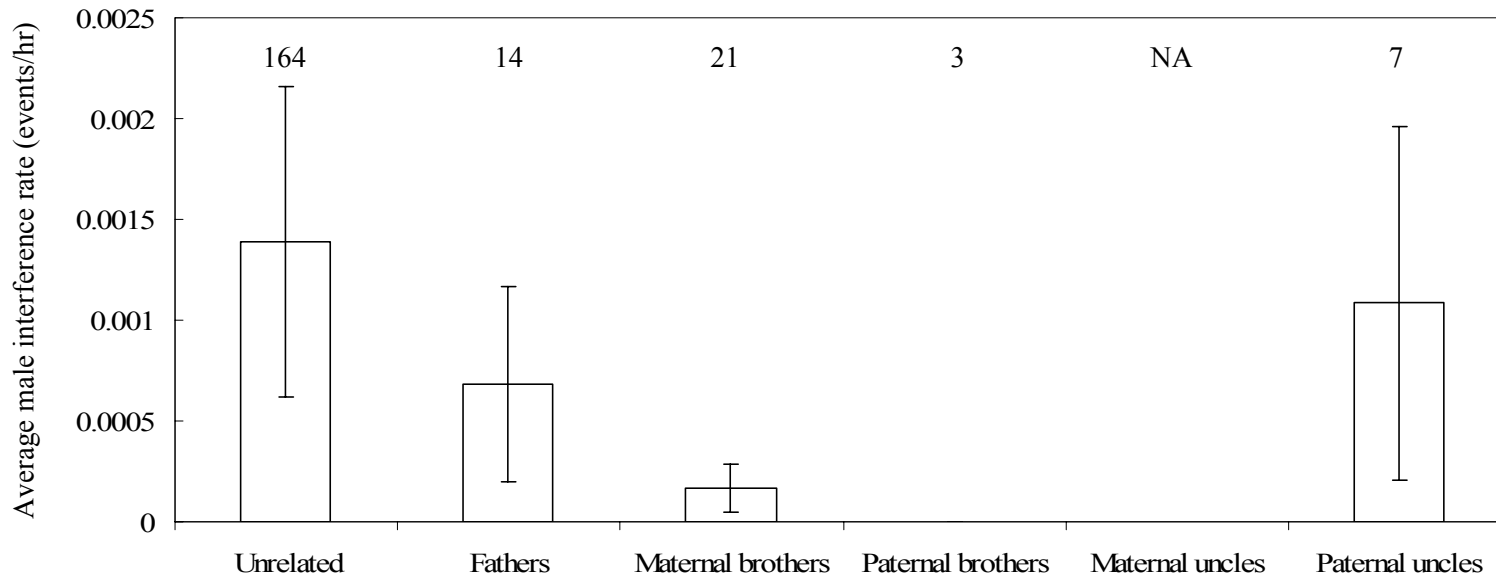
The average female responsiveness rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate \pm 1 SE.

Figure 3. 12. Male responsiveness by kin type



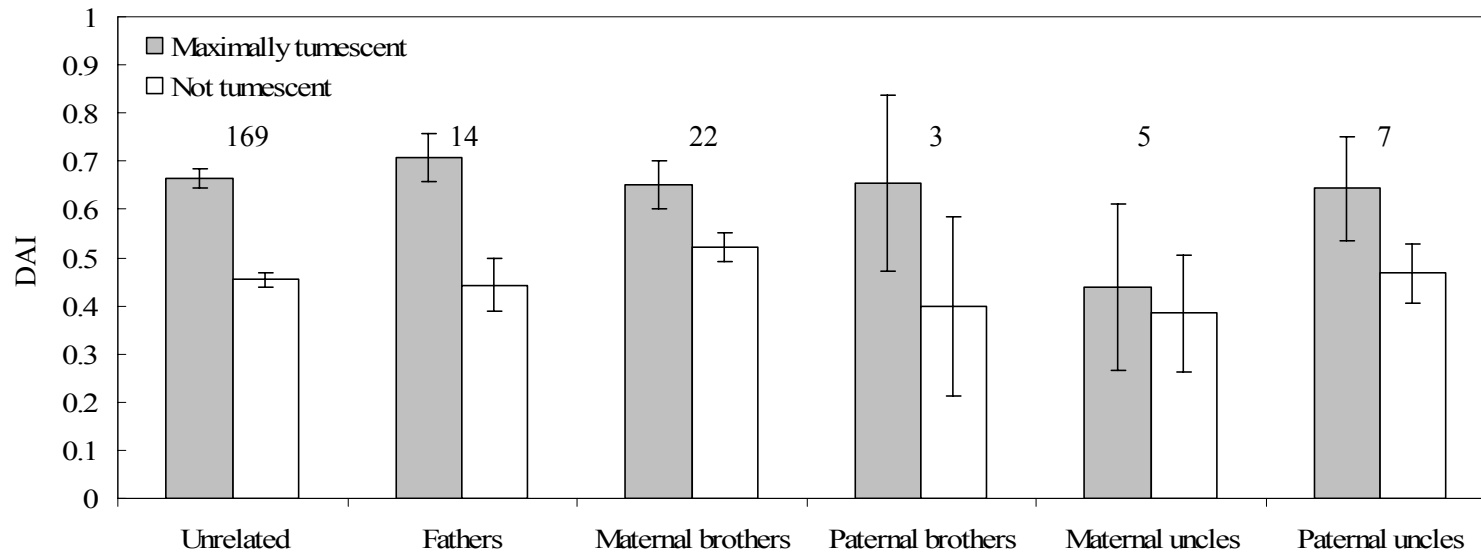
The average male responsiveness rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 13. Male interference by kin type



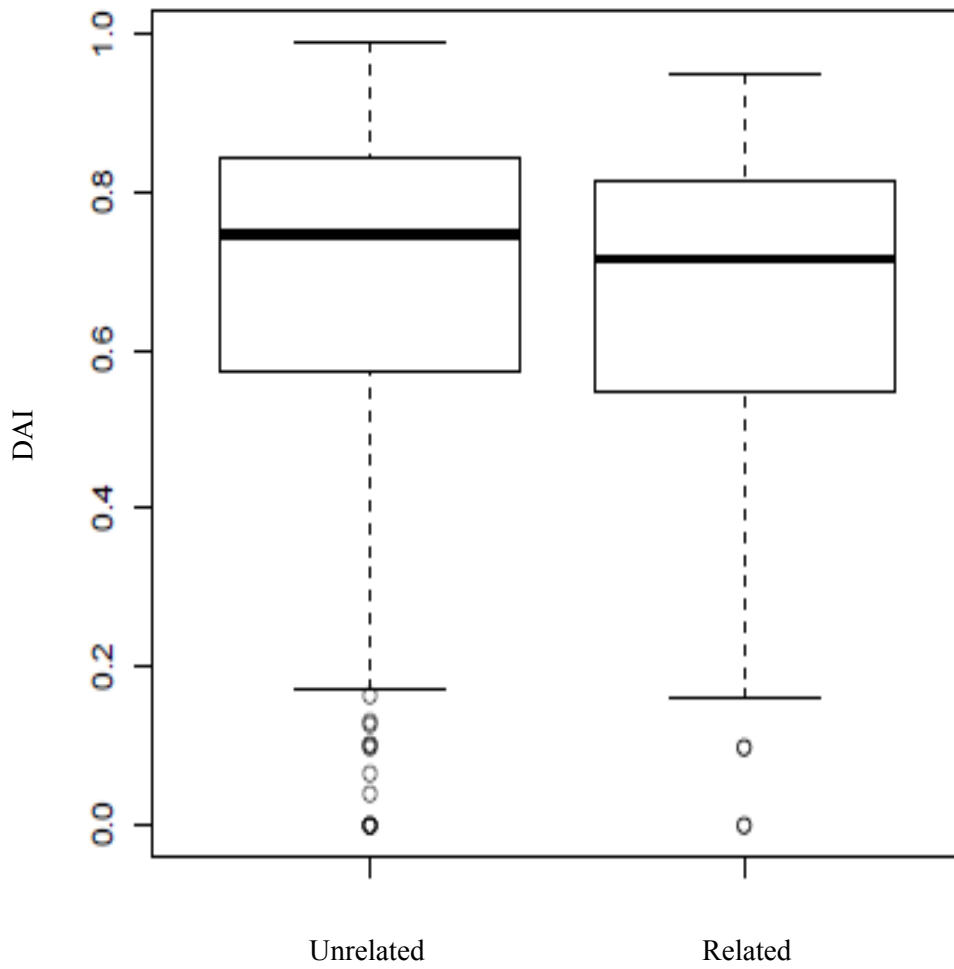
The average male interference rate for each kin type. Numbers are the number of unique male-female mating window data points available per kin type. NA means not applicable (females did not have any sexual activity with maternal uncles). Error bars indicate ± 1 SE.

Figure 3. 14. DAI by kin type



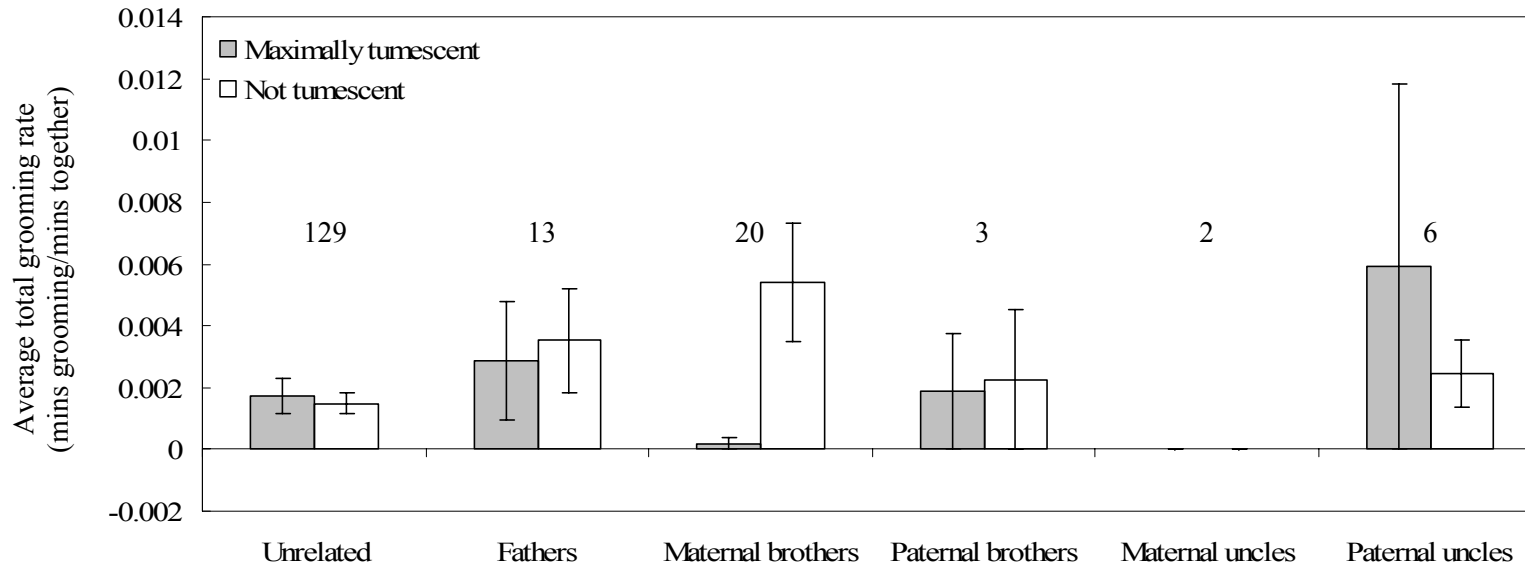
The average DAI for each kin type for both maximally tumescent days (i.e. sexually receptive) within mating windows and non-tumescent days within mating windows. Numbers are the number of unique male-female mating window data points available per kin type. Error bars indicate ± 1 SE.

Figure 3. 15. Boxplot of related and unrelated DAI



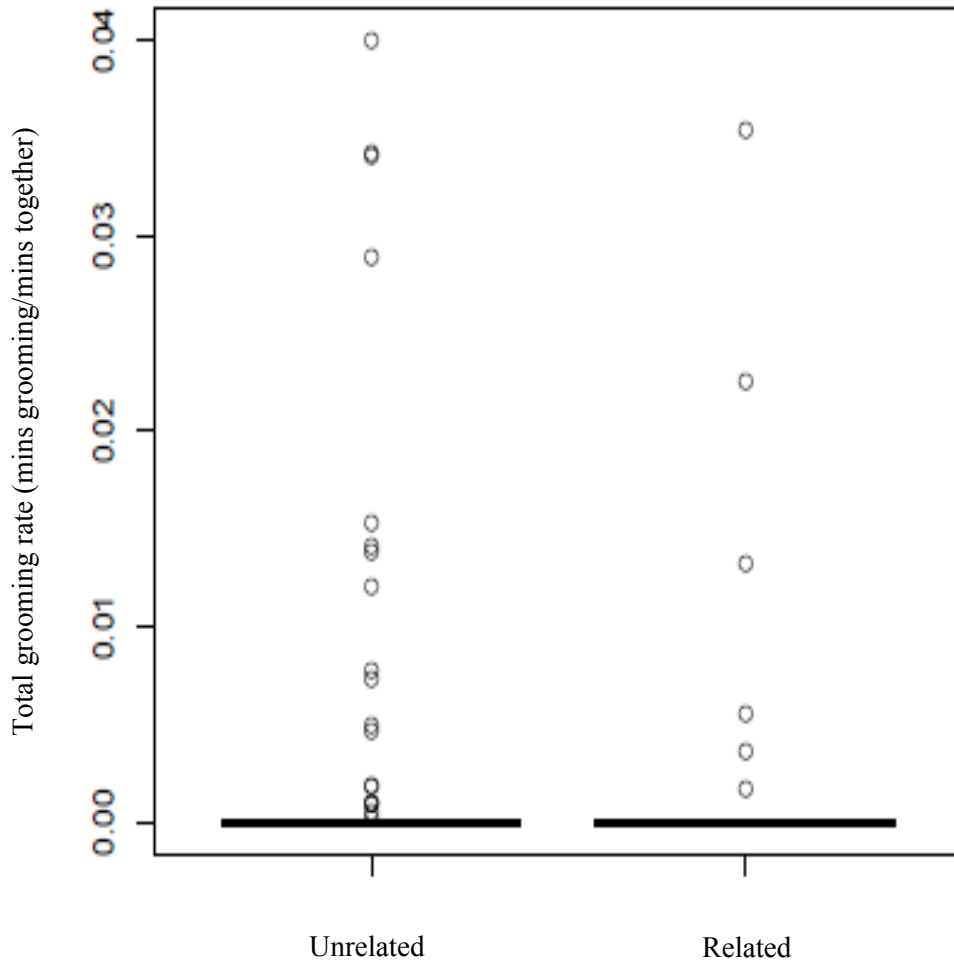
Boxplot of the DAIs for related and unrelated dyads during mating windows.

Figure 3. 16. Grooming by kin type



The average total grooming rate for each kin type for both maximally tumescent days (i.e. sexually receptive) within mating windows and non-tumescent days within mating windows. Numbers are the number of unique male-female mating window data points available per kin type. Error bars indicate ± 1 SE.

Figure 3. 17. Boxplot of related and unrelated grooming



Boxplot of the total grooming rates for related and unrelated dyads during mating windows.

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APPENDIX

Appendix 1: Genetic and Paternity Analyses¹

Sampling and DNA Isolation

All fecal samples were collected from individually recognized, habituated chimpanzees no more than several minutes after defecation. An equal volume of feces was transferred into a vial containing 25 ml of RNAlater (Ambion, Austin, Texas, U.S.A.), frozen in the field (4°C) as soon as possible until shipment, and then stored at -80°C in the laboratory. Samples used for analysis ranged from months to years old. We used the QIAamp DNA Stool Mini Kit (Qiagen, Valencia, CA, U.S.A.) to extract DNA from 400 µl to 2 ml of RNAlater preserved feces. Briefly, fecal samples were incubated in lysis buffer and spun, then the collected supernatant was treated with InhibitEX to remove potential PCR inhibitors. After spinning again, supernatants underwent proteinase K digestion, then were passed through a DNA binding column for DNA purification and final elution in 150–180 µl of elution buffer. Tissue samples were also stored in RNAlater and extracted using the DNeasy Tissue Kit (Qiagen).

Quantification of Fecal DNA

We determined DNA extract concentration using quantitative ('real-time') PCR before genotyping. Amplification reactions were performed as described in Morin et al. (2001) with minor modifications. BSA (bovine serum albumin, Ambion) was added between 10 µg and 40 µg (current protocol) per reaction. Duplicate sets of DNA standards of known quantity were used to generate a standard curve. Standard DNA amounts were 2000 µg, 1000 µg, 500 µg, 250 µg, 125 µg, 62.5 µg, 31.25 µg and 15.6 µg, and all amplification rounds included a 'no-template control'. Amplification and quantitative analysis were conducted using an ABI Prism 7700 Sequence Detector and its software, version 1.9 (Applied Biosystems, Foster City, CA, U.S.A.).

Microsatellite Analysis and Genotyping

All individuals for whom DNA samples were available were genotyped using at least 10 of 11 tetranucleotide microsatellite loci amplified by human primers. The 11 loci were a subset of those used by Constable et al. (2001) (D19S431, D9S905, D18S536, D10S676, D4S1627, D2S1333, D4S243, D1S548, D9S922, D11S1366, D2S1326) selected to be on different chromosomes or to avoid linkage by having a maximum of

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two markers per chromosome that were at least 50 cM apart (genetic maps from Marshfield Center for Medical Genetics, <http://research.marshfieldclinic.org/genetics/>).

Amplifications were performed in 20 ml reactions with at least 5 ml of fecal DNA extract. Reaction mixes were composed in one of two ways: (1) 1x AmpliTaq Gold PCR Master Mix (Applied Biosystems), 1.25 mM of additional MgCl₂, 0.25 mM of additional dNTPs, 0.2 mM of each primer and 25 mg of BSA; (2) (current protocol) 1x AmpliTaq Gold Buffer II, 4.375 mM of MgCl₂, 1.5 mM of dNTPs, 0.4 mM of each primer, 50 mg of BSA, 2.5 units of AmpliTaq Gold DNA polymerase, LD (Applied Biosystems). Amplification was performed on ABI Gene Amp PCR System 9700 thermocyclers using an initial denaturation of 95°C for between 2.5 and 5 min (current protocol), 12 cycles of 95°C for 30 s, 60°C (-0.5°C per cycle) for 30 s, 72°C for 30 s, followed by 45 cycles of 95°C for 30 s, 54°C for 30 s, 72°C for 30 s, and a single final extension at 72°C for 10 min.

The forward primer for each microsatellite locus was labeled with a FAM (Invitrogen, Carlsbad, CA, U.S.A.), HEX (Invitrogen) or NED (Applied Biosystems) fluorescent dye for allele sizing. PCR products were pooled into two groups with two of each fluorescent dye type of nonoverlapping product sizes: (1) D19S536 (FAM), D4S243 (FAM), D10S676 (HEX), D9S922 (HEX), D19S431 (NED) and AMEL 212 (NED) (see below); (2) D2S1326 (FAM), D2S1333 (FAM), D4S1627 (HEX), D9S905 (HEX), D1S548 (NED), D11S1366 (NED). A mix of 1.5 ml of pooled sample, 0.5 ml of a ROX (fluorescent dye)-labeled molecular weight ladder (Applied Biosystems), 1 ml of loading dye and 2.5 ml of formaldehyde was denatured at 95°C for 5 min, then immediately put on ice; 1.5 ml of this mix was then loaded onto a 6% GenePage Plus polyacrylamide gel (Amresco, Solon, OH, U.S.A.) and electrophoresed for 3.2 h at 51°C and 3000 V on an ABI Prism 377 DNA Sequencer (Applied Biosystems). Sizing of alleles was done using GeneScan software, versions 2.1 and 3.2.1 (Applied Biosystems). Repetition of genotyping for each locus was done, at a minimum, according to the recommendations of Morin et al. (2001) based on the amount of DNA per reaction, but the vast majority of reactions had well over 200 pg.

Sample Identity Verification

The accuracy of the sample identities and genotypes was ensured through several means. First, since mitochondrial DNA is inherited matrilineally, samples from individuals that were maternal relatives were confirmed to be of the same haplotype. Mitochondrial haplotypes were created by amplifying and directly sequencing a 498-base pair region of the hypervariable D loop using primers L15997 (50-CACCATAGCACCCAAAGCT-30) and H16498 (50-CCTGAAGTAGGAACCAGATG-30). PCRs were performed in 30 ml (current protocol) or 50 ml reactions containing 1x Expand Long Template PCR Buffer II, 0.58 (30 ml) or 0.35 (50 ml) mM of dNTPs, 1.33 (30 ml), 0.8 or 0.4 (50 ml) mM of each primer, 25 mg

of BSA, 2.5 units of Expand Long Template Taq polymerase and 5 ml of DNA extract. Thermocycling initially used the following conditions: initial denaturation of 5 min at 94°C followed by 55 cycles of 94°C for 30 s, 55°C for 1.5 min, 72°C for 30 s and a final extension of 72°C for 10 min. The protocol was later modified as follows: initial denaturation of 2 min at 94°C followed by 55 cycles of 94°C for 30 s, 55°C for 45 s, 68°C for 1 min and a final extension of 68°C for 10 min. Thirteen different haplotypes have been identified within the Gombe population (Liu et al. 2008). DNA samples were not quantified and genotyped if there was a mismatch between the chimpanzee ID of the sample and the mitochondrial haplotype.

Second, the sex of the sample donor was confirmed whenever possible through amplification of a region of the amelogenin gene using primers AMEL-F212 (50-ACCTCATCCTGGGCACCCTGG-30) and AMEL-R212 (50-AGGCTTGAGGCCAACCATCAG-30). Because of a known deletion on the X but not the Y chromosome, male chimpanzees amplify two products (212 and 218 base pairs) whereas female chimpanzees have a single amplification product (212 base pairs) (Sullivan et al. 1993). Amplification was conducted under the same conditions as the microsatellite PCRs except each reaction contained 0.25 or 0.5 mM of each primer. Samples were not analyzed if there was a mismatch between the sex of the chimpanzee named on the sample and the genetically determined sex.

Additionally, Mendelian inheritance of microsatellite alleles were confirmed by verifying that offspring and their known mothers shared at least one allele at every locus. Finally, the genotypes were confirmed using at least two independent fecal samples whenever more than one was available.

Paternity Analysis

Paternity was first examined through exclusion and confirmed using the likelihood-based program CERVUS 2.0 (Marshall et al. 1998). All genotyped candidate males, mothers and offspring were genotyped at a minimum of 10 of 11 loci with one exception; Mel was only genotyped at five loci (Constable et al. 2001), but it was unlikely that he was a father for the two offspring for which he was a candidate (TN and ZS). He was only 9 years old at the time of their conception, and he had two and three loci, respectively, mismatching with the offspring. We assigned paternity to a male based on exclusion when he was the only male that lacked mismatches with the offspring, given the offspring, mother and male genotypes, and all other male candidates had at least one mismatch. DIA was the only offspring that did not fit the criteria, having two males that lacked mismatches (maternal half-siblings), but CERVUS assigned paternity to one of these two males with high confidence (see below).

We used CERVUS to conduct likelihood-based paternity analysis. Paternity simulation was conducted under the following conditions: 100 000 simulation cycles, 1% error rate and confidence levels of 80% and 95%. The proportion of loci typed and

candidate males sampled was set to the specific conditions surrounding each conception. Furthermore, we ran simulations under three genetic environments for each conception for the genotype frequencies and proportion of candidate males sampled: (1) within-community candidate males only; (2) all candidate males for both the Mitumba and Kasekela communities (both habituated); and (3) all chimpanzees alive at the time of conception for both the Mitumba and Kasekela communities and an additional 50% unsampled male candidates to account for potential candidates from the nonhabituated Kalande community (Constable et al. 2001; Alberts et al. 2006; Boesch et al. 2006). The added 50% unsampled candidates was a conservative estimate and was probably disproportionately high for offspring born after 1999; the southern Kalande community has been in decline since 1999, and currently is believed to have only one adult male (Pusey et al. 2008a). There were two exceptions to these simulation conditions. We used the genotype frequencies of all individuals alive at conception for each of the three candidate sampling conditions for GM because we had only a single candidate male genotype available. We included an advanced simulation parameter to the simulations for DIA whereby we accounted for the four maternal brothers amongst the candidate pool (related 0.25 to each other) because simple exclusion could not differentiate between two of them.

Paternities were assigned for all 36 possible offspring (14 repeated from Constable et al. (2001) and 22 newly assigned). Paternities repeated from Constable et al. (2001) agreed with previous assignments. Paternities based on the exclusion method were in complete agreement with the paternity assignment from CERVUS under all three simulation conditions (Table A.1). CERVUS assigned paternity with at least 80% confidence, and with 95% confidence the majority of the time. The single exception was the 75% confidence assigned to the paternity of DIA under the simulation conditions using allele frequencies based on all the individuals alive at the time of conception and 50% unsampled male candidates. To investigate this dramatic drop in confidence from the previous two simulation conditions, we repeated the analysis using the same allele frequencies but removing the unsampled proportion of candidates (therefore leaving complete sampling of Mitumba and Kasekela candidates). Confidence was again 95%, indicating that the unsampled male candidates caused the lowered confidence.

Table A. 1. Results of CERVUS paternity analysis under three simulation conditions

				Kasekela Candidate Males		Kasekela-Mitumba Candidate Males		All Alive Kasekela-Mitumba and 50% Unsampled Males	
Offspring	Mother	Father	Next Fewest Mismatches	Males Sampled (Total)	PEP and Confidence	Males Sampled (Total)	PEP and Confidence	Males Sampled (Total)	PEP and Confidence
BRZ	BAH	KS	4	12 (12)	0.99965 95%	14 (14)	0.99957 95%	14 (21)	0.99987 95%
<i>CN</i>	CD	WL	3	11 (12)	0.99999 95%	12 (17)	0.99995 95%	12 (26)	0.99994 95%
COC	CD	FD	2	13 (13)	0.99954 95%	16 (16)	0.99970 95%	16 (24)	0.99965 95%
DIA*	DL	FE	0 [FO]; 1 [FR]	12 (12)	0.99230 95%	14 (14)	0.99354 95%	14 (21)	0.99682 75%
<i>DL</i>	(DM)	BE	1	8 (15)	0.93004 80%	9 (21)	0.93539 80%	9 (32)	0.95270 80%
FAM	FN	SL	2	13 (13)	0.99950 95%	16 (16)	0.99952 95%	16 (24)	0.99900 95%
<i>FE</i>	FF	EV	4	12 (12)	0.99993 95%	13 (17)	0.99993 95%	13 (26)	0.99992 95%
<i>FI</i>	FF	FR	1	12 (12)	0.99970 95%	14 (19)	0.99973 95%	14 (29)	0.99977 95%
FLI	FF	KS	2	13 (13)	0.99837 95%	15 (18)	0.99867 95%	15 (27)	0.99890 95%
<i>FN</i> †	FF	GB	4	5 (11)	0.99976 95%	5 (16)	0.99976 95%	5 (24)	0.99999 95%
FND	FN	SL	4	13 (13)	0.99984 95%	16 (18)	0.99986 95%	14 (27)	0.99978 95%
<i>FO</i>	FF	WL	3	11 (12)	0.99980 95%	12 (17)	0.99982 95%	12 (26)	0.99978 95%

				Kasekela Candidate Males		Kasekela-Mitumba Candidate Males		All Alive Kasekela-Mitumba and 50% Unsampled Males	
Offspring	Mother	Father	Next Fewest Mismatches	Males Sampled (Total)	PEP and Confidence	Males Sampled (Total)	PEP and Confidence	Males Sampled (Total)	PEP and Confidence
FS	FF	GB	3	7 (12)	0.99997 95%	7 (17)	0.99997 95%	7 (26)	0.99999 95%
FU	FN	SL	4	12 (12)	0.99989 95%	14 (18)	0.99993 95%	14 (27)	0.99998 95%
GA	GM	WL	2	13 (13)	0.99980 95%	14 (18)	0.99964 95%	14 (27)	0.99960 80%
GD	GM	AL	3	10 (11)	0.99964 95%	11 (17)	0.99953 95%	11 (26)	0.99966 95%
GIM	GM	TB	3	12 (12)	0.99997 95%	15 (15)	0.99999 95%	15 (23)	0.99999 95%
GLD	GM	FR	3	13 (13)	0.99999 95%	15 (18)	0.99999 95%	15 (27)	0.99999 95%
GLI	GM	FR	2	13 (13)	0.99922 95%	15 (18)	0.99932 95%	15 (27)	0.99974 95%
GM†*	(ML)	EV	NA	1 (16)	0.95759 95%	1 (19)	0.95760 80%	1 (29)	0.95759 80%
JK	JF	AL	3	11 (12)	0.00059 95%	12 (17)	0.99967 95%	12 (26)	0.99933 80%
MAM	MAK	GL	3	12 (12)	0.99698‡ 95%	15 (15)	0.99803‡ 95%	15 (23)	0.99948 95%
SAM	SA	FR	2	11 (11)	0.99980 95%	14 (16)	0.99991 95%	14 (24)	0.99996 95%
SDB	SW	FR	4	11 (11)	0.99997 95%	14 (16)	0.99997 95%	14 (24)	0.99997 95%
SHA	SR	WL	3	13 (13)	0.99998 95%	16 (16)	0.99998 95%	16 (24)	0.99997 95%
SI	SW	WL	5	11 (12)	0.99999 95%	12 (17)	0.99998 95%	12 (26)	0.99999 95%

				Kasekela Candidate Males		Kasekela-Mitumba Candidate Males		All Alive Kasekela-Mitumba and 50% Unsourced Males	
Offspring	Mother	Father	Next Fewest Mismatches	Males Sampled (Total)	PEP and Confidence	Males Sampled (Total)	PEP and Confidence	Males Sampled (Total)	PEP and Confidence
SN	SA	AO	4	12 (12)	0.99998 95%	14 (19)	0.99999 95%	14 (29)	0.99999 95%
SR	SA	BE	4	11 (12)	0.99969 95%	12 (17)	0.99960 95%	12 (26)	0.99980 95%
TA	PI	GB	3	11 (12)	0.99996‡	12 (17)	0.99994‡	12 (26)	0.99992 95%
TN	PI	FR	2 [MEL]; 3	13 (13)	0.99961‡	14 (18)	0.99962‡	14 (27)	0.99984 95%
TOF	TTA	SL	3	11 (11)	0.99989‡	14 (16)	0.99993‡	14 (24)	0.99990 95%
TOM	TA	KS	3	11 (11)	0.99973 95%	14 (16)	0.99972 95%	14 (24)	0.99982 95%
TZN	PI	FR	2	13 (13)	0.99950‡	16 (17)	0.99947‡	16 (26)	0.99996 95%
YAM	YD	WL	2	13 (13)	0.99834 95%	15 (18)	0.99873 95%	15 (27)	0.99928 95%
ZEL	TZ	KS	3	13 (13)	0.99992 95%	16 (17)	0.99991 95%	16 (26)	0.99996 95%
ZS	TZ	FR	2	13 (13)	0.99987 95%	14 (18)	0.99992 95%	14 (27)	0.99984 95%

PEP is the paternity exclusion probability. Offspring in bold italics had paternities previously established by Constable et al. 2001; offspring GLD and GLI are twins and were treated as a single paternity in the priority of access analysis. Parentheses around the mother's ID indicate she was not genotyped. MEL was the only candidate male genotyped at less than 10 loci. The top three candidate males for DIA's paternity are all maternal brothers (FE, FO, FR).

† Offspring were not included in the priority of access analysis because their conceptions preceded 1984.

* Paternity analysis was done slightly differently; see Paternity Analysis in the Appendix 1 for details.

‡ Offspring, candidate male, and mother genotypes were compared at less than 10 loci because maternal alleles were not in the candidate male allele frequencies.