

The Evolution of Extended Sexual Receptivity in Chimpanzees: Variation, Male-Female Associations, and Hormonal Correlates

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

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Abstract

Sexual conflict occurs when female and male fitness interests diverge. In a social system characterized by aggressive sexual coercion and the risk of infanticide, female chimpanzees (*Pan troglodytes*) respond to this conflict by exhibiting an exaggerated sexual swelling that advertises sexual receptivity while concealing the exact timing of ovulation. Sexual swellings impose significant costs, yet can persist into pregnancy. Records from long-term studies of eastern chimpanzees (*P. t. schweinfurthii*) in Gombe National Park, TZ, and Kibale National Park, UG, provide data on post-conception swellings, while data on group composition and behaviors such as mating, grooming, and aggression are drawn from the Gombe database only. Throughout, I use linear mixed models to simultaneously test multiple effects while controlling for repeated measures of individuals. In Chapter 1, I tested whether variation in females' vulnerability to infanticide and aggression predicted the amount of swelling during pregnancy. In Chapter 2, I examined female-male relationships across reproductive states to ask whether females can better gain benefits and avoid costs by affiliating promiscuously with all males, or by investing in relationships with preferred males. Finally, I analyzed metabolites of reproductive hormones using enzyme immunoassay of urinary metabolites of reproductive hormones from pregnant females in both populations to build a hormonal profile of post-conception swellings. Swellings during pregnancy increase female-male association, and are caused by the same basic hormonal mechanism as pre-conception swellings, though they occur in a very different hormonal milieu. Females at greater risk

of infanticide and intrasexual aggression swell more during pregnancy. Females mate promiscuously before conception, but during pregnancy and lactation, preferentially groom with males that are likely to protect them from aggression and infanticide. Based on these and other findings, I conclude that post-conception swellings in chimpanzees are an adaptive response to sexual conflict.

Dedication

This dissertation is dedicated to Dr. Mary Ellen Newport, whose exuberance and awe for biology opened the door to my own; and to all my teachers at Maumee Valley Country Day School, who are also my family.

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1. Introduction: Deceptive signaling in mating and extended receptivity in primates

Sexually selected signals of mate quality have classically been described as handicaps, communicating to prospective mates that the bearer is of high enough quality to have borne the cost of the signal (Zahavi, 1975). The evolution of dishonest signals is theoretically limited by the costs involved in producing them, and the eventual degradation of meaning therein; however, cheating can still occur in an evolutionarily stable system (Grafen, 1990). Sexual conflict occurs when male and female fitness interests oppose in part or in full (Trivers, 1972), and can favor deceptive signaling between the sexes. For instance, female long-tailed dance flies (*Rhamphomyia longicauda*) depend on male nuptial gifts for proteins. Males are interested in mating only with females carrying mature eggs, so females inflate specialized abdominal sacs to create the illusion of gravidity and attract mates (Funk and Tallamy, 2000). In the European bitterling fish (*Rhodeus amarus*), females perform deceptive oviposition, inducing males to ejaculate without actually ovipositing (Smith et al., 2007). Female poison dart frogs (*Dendrobates auratus*) use pseudo-courtship as a form of mate guarding, to distract their male partners from mating with an intruding female, also without subsequent oviposition (Summers, 2014). Male peacocks perform deceptive copulation hoots to draw females toward a lek to mate (Dakin and Montgomerie, 2014).

Extended female sexual receptivity, or mating beyond the periovulatory period, can be interpreted as such a deceptive signal, since it incites male mating effort but offers no reproductive benefit to the male (Searcy and Nowicki, 2005). Extended receptivity occurs frequently in birds (Birkhead et al., 1987), and primates (Wrangham, 1993), as

well as in other animal taxa. Nonconceptive mating can function as practice (in spiders: Pruitt and Riechert, 2011), play (in pigs: Berry and Signoret, 1984), pair-bonding (in birds: Birkhead et al., 1987), or paternity confusion (in primates: Blaffer Hrdy, 1977; Palombit, 2012).

Among anthropoid primates, sexual receptivity is often advertised visually through the swelling of a specialized anogenital skin (Dixson, 1983). These fluid-filled, hormonally mediated swellings vary across primate taxa in the honesty and reliability of information that they convey about female fertility; the diversity of sexual swellings in primates and their relationship to reproductive events is discussed in depth in Chapter 3. Sexual swellings can contribute to extended receptivity in a variety of ways. Most simply, they can extend beyond the periovulatory period, during which matings are mostly likely to lead to conception; in this way, the swellings are “exaggerated” (Nunn, 1999). In addition, females may exhibit multiple swellings before conceiving. Repeated, nonconceptive swellings may be the result of energetic constraints on ovarian function (Nepomnaschy et al., 2004; Emery Thompson et al., 2012). Nonetheless, nonconceptive swellings generate additional mating opportunities for females; chimpanzees may copulate hundreds of times before conceiving (Goodall, 1986; Wrangham, 2002). Finally, sexual swellings can occur during pregnancy, when conception is impossible, but females may still gain social or fitness benefits from engaging in mating behavior. The focus of this dissertation is sexual receptivity as mediated by sexual swellings in pregnant chimpanzees (*Pan troglodytes*). In species that lack sexual swellings, extended receptivity can also take the form of behavioral estrus. Here, I discuss the occurrence of

extended receptivity in a variety of taxa and the proposed functions thereof, with an emphasis on paternity confusion for infanticide avoidance.

1.1 Extended receptivity in primates

In response to the threat of infanticide, selection for extended receptivity can lead to mating after conception, or, more commonly, to a prolonged period of mating before conception. Vervet monkeys (*Cercopithecus aethiops*) exhibit no behavioral estrous and no cyclical changes to the perineum, effectively concealing ovulation. However, hormonal data reveals that their seasonal mating behavior begins nearly two months before the onset of ovulatory cycles, and that most females conceive in the first ovulatory cycle (Andelman, 1987). Females continue to copulate for ~17 weeks after conception, and these copulations are initiated by males (Andelman, 1987). In fact, females were more receptive to males' mating attempts during early pregnancy than in the early months of the breeding season (Andelman, 1987). Andelman speculates that by concealing ovulation, females reduce the value to males of any one copulation, reducing male-male competition, including infanticide (Andelman, 1987). The first swellings following lactational amenorrhea in captive lion-tailed macaques (*Macaca silenus*) were significantly longer than later cycles, and females copulated and called at higher rates during these early cycles (Clarke et al., 1993). While long follicular phases in *Pan* are associated with low estrogen production (Dahl et al., 1991) and could result from energetic constraints following lactation (Thompson et al., 2012), extended early swellings in lion-tailed macaques could function to attract extra-group males and confuse paternity during nonconceptive cycles (Clarke et al., 1993).

Even in strepsirrhine primates, characterized by strict hormonal control of estrus, mating can occur outside the period of peak estradiol (E_2) production that typically accompanies behavioral estrus. In sifakas (*Propithecus verreauxi*), anestrus females have been observed to mate with new resident males and recently deposed males (Brockman and Whitten, 1996). This behavior was hypothesized to represent the females' attempts to reduce the risk of infanticide by males with whom she had not mated during estrus.

Capuchin monkeys (*Cebus capucinus*) have been observed to copulate extensively during pregnancy (Manson et al., 1997). Pregnant females were more receptive to subordinate than alpha males, but alpha males were involved in the majority of observed copulations with cycling, non-pregnant females (Carnegie et al., 2005). Pregnant females also initiated more grooming bouts with subordinate males than did females in other reproductive states. The authors suggest that pregnant females may direct their mating and grooming efforts at subordinate males in order to confuse paternity and reduce the risk of infanticide (Carnegie et al., 2005). Post-conception estrus was associated with changes to the social group in patas monkeys (*Erythrocebus patas*), and occurred more frequently in primiparous females' pregnancies than in multiparous females' pregnancies (Loy, 1981). During a period of high infanticide risk, post-conception copulations were observed in red colobus monkeys (*Colobus badius tephroceles*); females in all reproductive states were more proceptive toward the infanticidal male during this time (Struhsaker and Leland, 1985). Furthermore, this strategy appears to have worked: none of the infants whose mothers had copulated with the infanticidal male, while pregnant or

ovulating, were killed. None of the females who had mated with the infanticidal male before conceiving copulated during pregnancy (Struhsaker and Leland, 1985).

Post-conception estrus can also be highly stereotyped and insensitive to social factors, like the presence of new immigrant males, as in Hanuman langurs (*Semnopithecus entellus*) (Sommer et al., 1992). These females are hypothesized to compete for the resident male's sperm; by mating during pregnancy, females reduce the number of potential future competitors for themselves and their offspring (Sommer et al., 1992). The same hypothesis has been proposed in western gorillas (*Gorilla gorilla*), where pregnant females are more likely to mate on days when cycling females are mating (Doran-Sheehy et al., 2009). Pregnant blue monkeys (*Cercopithecus mitis*) also frequently mate during pregnancy, though this behavior is not affected by the number of males, presence of a new male, or recent influx of immigrant males in the group (Pazol, 2003).

An important component to determining whether a sexual signal is truly deceptive is the response of the receiver. Evidence from several species suggests that males can discriminate between pre- and post-conception swellings using visual, olfactory, or behavioral cues. Sooty mangabeys (*Cercocebus torquatus atys*) exhibit a single, stereotyped perineal swelling approximately 49 days following conception (Gordon et al., 1991). As in preconception cycles, post-conception swellings are associated with a high ratio of estrogens to progesterones, and females mate multiply during them. However, further work shows that alpha males do not mate with pregnant estrous females, and may use differences in the patterns of estrogen and progesterone peaks to discriminate between fertile and infertile cycles (Gordon et al., 1991; Gust, 1994). In a related species,

Tana River crested mangabeys (*C. galeritus galeritus*), post-conception swellings were also very consistent, but were paler in color and deflated more slowly than fertile swellings; however, pregnant females did copulate while swollen (Kinnaird, 1990). Similarly, in captive golden-bellied mangabeys (*C. agilis chrysogaster*), post-conception swellings lasted longer and detumescence was more gradual than in pre-conception swellings (Walker et al., 2004). Male patas monkeys mated approximately equally with pre- and post-conceptive females; however, pregnant estrous females were less proceptive than non-pregnant estrous females, performing significantly fewer solicitations (Loy, 1981). Only low-ranking male red-tailed monkeys (*Cercopithecus ascanius*) consorted with pregnant females (Cords, 1984). The tendency for young or low-ranking males to mate during infertile windows can be interpreted as a female strategy for paternity confusion or as the inability of these less-experienced males to successfully identify fertile mating opportunities.

Post-conception swellings have also been reported in Southern pigtail macaques (*Macaca nemestrina*), Japanese macaques (*M. fuscata*), rhesus macaques (*M. mulatta*), mandrills (*Mandrillus sphinx*), and drills (*M. leucophaeus*) (Hadidian and Bernstein, 1979; Soltis et al., 1999). Nearly 80% of pregnant Barbary macaques (*M. sylvanus*) showed post-conception swellings in one study of promiscuous mating behavior; females continued to copulate during pregnancy (Small, 1990). Post-conception mating has also been observed in mantled howling monkeys (*Alouatta palliata*), which exhibit sexual swellings before but not after conception. However, post-conception mating seems to be rare, and therefore difficult to interpret functionally (Glander, 1980).

1.2 Sexual swellings and extended receptivity in chimpanzees and bonobos

Female chimpanzees exhibit exaggerated swellings that last for 10-14 days in their ~35-day ovarian cycle (Elder and Yerkes, 1936; Tutin, 1979; Wallis, 1997; Matsumoto-Oda, 1999a; Emery and Whitten, 2003). Mating is virtually restricted to periods of maximal tumescence (Wallis, 1992). Furthermore, several studies indicate that subtle cues distinguish the periovulatory period within the period of maximal tumescence, and that males are sensitive to these cues, mating more frequently during conceptive cycles and on the most fertile days within cycles (Matsumoto-Oda et al., 2003; Deschner et al., 2004; Emery Thompson and Wrangham, 2008). Nonetheless, females are able to mate outside of the periovulatory period and in nonconceptive cycles. The number of cycles to conception (CTC) varies among subspecies; western chimpanzees (*P. t. verus*) tend to cycle for longer before conceiving than do eastern chimpanzees (*P. t. schweinfurthii*) (Wrangham, 2002). The cost-of-sexual-attraction hypothesis, proposed by Wrangham in 2002, offers an ecological explanation for the observed difference, whereby higher food availability in West African habitats reduces the relative cost of the decreased foraging efficiency associated with sexual receptivity (Wrangham and Smuts, 1980). Because extending the period of sexual receptivity confers benefits to females, females who can “afford” to utilize this strategy should do so, leading to variation among females and between populations in CTC.

Chimpanzees also extend sexual receptivity into pregnancy: Sexual swellings are most commonly observed in the first trimester, but can continue throughout gestation. They have been recorded in both captive (Yerkes and Elder, 1937; Wallis and Lemmon,

1986; Dahl, 1999) and wild (Wallis and Goodall, 1993) studies. In captivity, males solicited copulations more frequently from fully swollen pregnant females than from fully swollen, cycling females, and pregnant females were more receptive than their cycling counterparts (Wallis and Lemmon, 1986). Many hypotheses have been proposed for the function of infertile swellings, both before and after conception (reviewed in Morin, 1993).

Even in light of the extended receptivity observed in chimpanzees, bonobos (*P. paniscus*) are undoubtedly the primates best known for nonconceptive sex. Early reports included sociosexual behaviors between dyads of adult females, adult males, and adults and juveniles of both sexes (Kano, 1980). Among potentially conceptive pairs, copulation has been observed for food sharing (Kano, 1980) and alleviation of tension (Manson et al., 1997). Bonobo females have sexual swellings that are adapted for ventro-ventral contact (Kano, 1992; Dixson, 2012); analysis of steroid hormone production in relation to full swelling showed that the timing of ovulation varies, but always occurred in the last half of full swelling, offering a probabilistic signal of fertility to males (Reichert et al., 2002). Bonobos extend receptivity in a number of ways: The ovarian cycle is longer in bonobos than in chimpanzees, and females are fully swollen for a longer proportion of the cycle (Dahl et al., 1991; Wrangham, 1993). Furthermore, females have been observed to copulate outside the period of maximal tumescence (Reichert et al., 2002; Furuichi and Hashimoto, 2004). Females exhibit their first swellings at a younger age than chimpanzees and resume cycling soon after birth (Kano, 1992; Furuichi, 2011). They also swell throughout pregnancy, as late as one month before parturition (Kano, 1992). As a

result of all of these factors, female bonobos spend a larger part of their reproductive lives in a fully tumescent state relative to female chimpanzees. The peaceful, female-dominant society found in bonobos may be partly explained by females' extended receptivity, which reduces the efficacy and intensity of male-male competition and sexual coercion (Furuichi, 2011).

1.3 Outline of chapters and hypotheses

In this dissertation, I first test adaptive and non-adaptive hypotheses for the evolution of post-conception swellings in eastern chimpanzees by analyzing variation among females in this trait. Specifically, I ask whether females' vulnerability to male infanticide and female aggression predicts the frequency of sexual swellings during pregnancy. Then, I use measures of association between males and females to test whether these relationships are best explained by a purely promiscuous female strategy of paternity confusion, or whether females can gain protection by investing preferentially in relationships with particular males. Finally, I analyze urinary estrogen and progesterone metabolites collected from pregnant females to compare the hormonal profile of pre- and post-conception swellings: Selection for sexual receptivity during pregnancy is likely to act on production of estrogen and progesterone, and understanding this mechanism will contribute to understanding the evolution of extended receptivity in chimpanzees.

1.4 Field sites and general data collection methods

I present data from two field sites encompassing three communities of eastern chimpanzees. Gombe National Park is situated on the eastern shore of Lake Tanganyika in northwest Tanzania. Only 35 km², Gombe National Park is a narrow rectangle

encompassing a series of streambed valleys running east to west from the rift escarpment to the lake. The terrain is steep and rocky, with a wide variety of ecotypes: evergreen forests, gallery forests, open woodlands and grasslands on the hilltops (Goodall, 1983). Three chimpanzee communities live in the park; the central (Kasekela) and northern (Mitumba) communities are habituated; a third, unhabituated community inhabits the southern end of the park and is monitored through non-invasive fecal sampling (Rudicell et al., 2010). Data in this dissertation come from the habituated communities of Kasekela and Mitumba. Habituation of the Kasekela community began in 1960 when Jane Goodall established a camp and began observing the chimpanzees from a distance (Goodall, 1983). In 1963, a central feeding station was established and chimpanzees began to visit daily to receive bananas. Observations at the feeding station became part of the A-record; observers noted attendance, female estrous state, grooming, copulation and agonistic behaviors. The frequency and quantity of bananas provided were systematically reduced until feeding ended completely in 2000. All-day focal follows of individuals outside of the feeding station began in the early 1970s and have been conducted continuously to the present (Goodall, 1986; Wilson et al., 2012). These observations comprise the B-record. Research assistants record group composition every 15 minutes, estimating arrivals of individuals to the focal group to the nearest 5-minute interval, food type during feeding, and encounters with other species. They also note the size of the sexual swelling in females on a fractional scale of 0-1, where 0 is no swelling, 0.25-0.75 represent partial swelling, and 1 is full swelling. Long-hand narrative notes contain information on basic activity of the focal, such as travel and feeding, as well as copulations and other

behaviors of interest among all group members. Grooming with the focal individual was recorded in 5-minute scans from 1978-1997, and in long-hand notes from 1998 to present. Agonistic interactions in the group, including all occurrences of submissive pant-grunt vocalizations, are also recorded in the long-hand notes and used to calculate dominance rank. All individuals are known visually by research assistants. Habituation of the Mitumba community began in 1988. All individuals were known by 1995, and field assistants now perform daily focal follows according to the same protocol as described here for the Kasekela community. Both teams record the position of the focal party using maps and, more recently, GPS units.

Kibale National Park is located in western Uganda; the terrain is hilly and ecotypes range from lowland rainforest to montane forest. Kibale's Kanyawara community has been studied since 1983 (Chapman and Wrangham, 1993) and has been under continuous observation by the Kibale Chimpanzee Project since 1987; all individuals were habituated by 1990 (Machanda et al., 2013). Pairs of field assistants conduct daily group follows, noting the group composition, which includes all individuals within 50 m, following a chain rule (Machanda et al., 2013). Female estrous state is recorded as 1 (no swelling), 2 (partial swelling) or 3 (full swelling) (Emery and Whitten, 2003). Individuals in the group are targeted for rotating ten-minute focal follows including the activity of other individuals within five m. If the group fissions during a focal follow, field assistants remain with the party of the focal individual (Machanda et al., 2013).

2. Variation in Post-conception Swellings Reflects Female Vulnerability to Infanticide and Aggression

2.1 Introduction

Sexual swellings occur in chimpanzees and in many other primate taxa, most commonly in the Old World primates, and are well studied as signals of female fertility, sexual receptivity, and condition (Dixson, 1983; Douglas et al., 2016; Street et al., 2016). When the signal is exaggerated, extending beyond the periovulatory period, it is thought to serve dual functions: Females can mate with preferred males around ovulation to achieve fertilization, and with other males during less fertile times to achieve other social goals (Nunn, 1999). In some species, as described in the introductory chapter, swellings can also occur after conception, and may offer an extension of the social benefits gained during “normal” cycling. Given the stark social and sexual behavioral changes associated with sexual swellings in chimpanzees, it seems most likely that any social benefits of post-conception swellings are associated with male-female relationships and the services that males may provide to their female social partners. Paternity confusion for male infanticide avoidance is a commonly identified strategy among female primates (reviewed in Palombit, 2012). Sexual swellings also aid in females’ integration into new communities following dispersal (Pusey, 1980; Wallis, 1992; Deschner and Boesch, 2007; Kahlenberg et al., 2008b). The extreme variation within and among females in the expression of post-conception swellings has contributed to the enigma of this phenomenon, but may also provide the key to deciphering its adaptive value. Here, I ask whether predictors of female vulnerability to infanticide and intrasexual aggression can explain variation in the occurrence and extent of post-conception swelling.

2.1.1 Infanticide in primates and the paternity confusion hypothesis

Hrdy was among the first to argue that infanticide by “usurping” males was not pathological nor simply a result of overcrowding, but an adaptive strategy by which males maximized their reproductive success during their relatively short windows of access to females (Blaffer Hrdy, 1977; Hrdy, 1979). Although male infanticide is rare, and even more rarely observed, available data across species support the sexual selection hypothesis; these lines of evidence have expanded in recent years to include behavioral, hormonal, and genetic data (Hrdy, 1979; Palombit, 2015). Phylogenetic analysis supports the conclusion that infanticide evolves most frequently in mammalian species living in stable male-female groups, where reproduction is aseasonal and periods of lactational amenorrhea are long (Lukas and Huchard, 2014).

However, counterstrategies such as pair-bonding and male-female affiliation do not appear to have evolved in response to infanticide. Rather, female promiscuity and associated increases in male testis size are more likely to arise following the evolution of infanticide in a particular lineage (Lukas and Huchard, 2014). The strategy of paternity confusion is so effective that infanticide is more likely to be subsequently lost once testis size increases (Lukas and Huchard, 2014).

While infanticide is an effective strategy for males, it imposes severe fitness costs on females. For example, it can lengthen the interval between surviving offspring (Swedell et al., 2014), and females may suffer serious injury and death while defending their offspring from infanticidal males (Singh et al., 2014). Therefore, female counterstrategies are predicted to evolve in response. Species that live outside of

permanent social groups may use physical avoidance of conspecifics as a defense against infanticide (Singh et al., 2014), but this option is not available to group-living primates. Other mammal species may achieve paternity confusion through communal nesting, which provides the added benefit of shared nest defense (Auclair et al., 2014). Post-conception mating behavior can function as a female counterstrategy to infanticide in platyrrhines and catarrhines (Palombit 2012).

The sexual selection hypothesis for infanticide is well-supported in chimpanzees (Hamai et al., 1992; Hiraiwa-Hasegawa and Hasegawa, 1994; Murray et al., 2007b; Nakamura and Itoh, 2015). In Gombe, the current alpha male has attacked or killed three infants born to a single female, all of whom were almost certainly conceived while she was with other, lower-ranking males during exclusive consortships away from the group (Mjungu et al., 2014; unpublished data). Alternative hypotheses for infanticide have also been proposed in chimpanzees. Males in neighboring groups may kill infants in order to drive the competing community away from border areas and ultimately expand their own range (Mitani et al., 2010), or to induce young females to disperse (Goodall, 1986). Resident males may use extreme aggression and infanticide as a form of sexual coercion to monopolize mating in subsequent cycles (Hamai et al., 1992). In one example, the mother of an infanticide victim was observed to associate more with male attackers following the attack (Arcadi and Wrangham, 1999). One potentially effective defense against infanticide is simply to avoid associating with males, a strategy available to female chimpanzees living in fission-fusion societies (Otali and Gilchrist, 2006).

Therefore, one hypothesis for the function of post-conception swellings is that female chimpanzees benefit from exaggerated swellings by mating widely over an extended period of time, thereby confusing paternity and reducing the likelihood of infanticide by males. Extending the period of apparent sexual receptivity into gestation enhances these benefits, especially for females who have failed to confuse paternity before conception. Females with fewer cycles to conception, and females who conceived on consortship, will have more swollen days during pregnancy due to their reduced opportunity to mate widely before conception. Other factors may limit females' ability to mate widely before conceiving, putting them at greater risk of infanticide later, and increasing the benefits of swelling during pregnancy. Young females are less attractive to males (Muller et al., 2006), and therefore may need to extend the receptive window to achieve paternity confusion. Recently immigrated females who have not mated extensively with resident males are also expected to swell more during pregnancy. Finally, this hypothesis predicts that infanticide by males is more likely following gestations with few or no swellings.

2.1.2. Intrasexual aggression in chimpanzees and the social passport hypothesis

The social passport hypothesis is another, non-mutually-exclusive hypothesis for the function of exaggerated swellings. It posits that swellings engender male interest and support for females, which would be especially important for new immigrants as they attempt to integrate into their adult communities (Deschner and Boesch, 2007). Recent immigrants in Gombe have been observed to associate closely with resident males, who also intervene in attacks by resident females (Pusey, 1990). These attacks can be extreme

and violent, and can even prevent females from successfully immigrating, making male support extremely valuable (Pusey et al., 2008). The same pattern has been observed in Kanyawara, where resident males offer support against aggressive resident females (Kahlenberg et al., 2008b). In mountain gorillas (*Gorilla beringei beringei*), where females also disperse, silver back males are crucial social partners for immigrant females, intervening in attacks by resident females, possibly as a mating tactic to encourage them to stay in the group (Watts, 1992). Much of female-female aggression in chimpanzees is related to space-use and access to resources. In Kanyawara, females with high-quality core areas were most aggressive to new immigrants (Kahlenberg et al., 2008a); Gombe females are more aggressive to other females within their own core areas (Miller et al., 2013). Intrasexual aggression is, therefore, a real threat to female reproductive success and survival. Post-conception swellings may help to garner male protection from female aggression during pregnancy and after birth. Because low-ranking females are more susceptible to aggression and infanticide by females, I expect that low-ranking females will swell more during pregnancy to counteract this risk. Recent immigrants, who have not yet established core areas and who may still face resistance from residents, will also swell more during pregnancy according to this hypothesis.

In order for post-conception swellings to provide the benefits proposed in the adaptive hypotheses above, they should also facilitate increased association between males and females. Therefore, I predict that females who swell more during pregnancy will also have higher dyadic associations with male partners.

2.1.3. Non-adaptive hypotheses for post-conception swellings

Non-adaptive hypotheses may provide a more parsimonious explanation for the phenomenon of post-conception swellings in chimpanzees. Reproductive function is tightly linked to energy availability, which can be measured non-invasively in wild animals using urinary c-peptide, a by-product of insulin production (Ellison, 2001; Sherry and Ellison, 2007). C-peptide is cleaved off the precursor molecule and therefore is produced and excreted in equal proportion to insulin, which is produced by the body in response to rising blood sugar (Kitabchi, 1977). In chimpanzees, urinary c-peptide levels reflect seasonal food availability and social stressors (Emery Thompson et al., 2009). Lactational amenorrhea, known to be mediated by energetic investment toward lactation and away from ovarian cycling, has also been linked to c-peptide. As lactation tapers off toward weaning, energy availability, as measured by c-peptide, rises, and this increase predictably precedes resumption of cycling (Emery Thompson et al., 2012). Body mass data from Gombe show that the chimpanzees' physical condition is correlated with monthly rainfall, which likely increases food availability. Body mass was highest in December through February and lowest in September, near the end of the dry season (Pusey et al., 2005). Even after the end of lactational amenorrhea, females may become acyclic during times of food scarcity, and females are more likely resume cycling and conceive during the late dry season, as they return to positive energy balance (Goodall, 1986; Wallis, 1995). Following these lines of evidence, it is possible that the variation in post-conception swellings is due to energetic constraints. According to this hypothesis, access to high-quality resources, due to environmental availability or individual

competitive ability, would best explain variation in cycling; this yields two predictions: High-ranking females will swell more during pregnancy, and there will be more swollen post-conception days during the late dry and early wet seasons than during the dry season.

Swellings are triggered by estrogen and inhibited by progesterone, both of which are elevated in pregnancy (Faiman et al., 1981; Dixson, 1983). Dahl (1999) documented higher levels of pathological outcomes, such as stillbirth and maternal abandonment, following gestations with little swelling, suggesting that swellings during pregnancy may reflect hormonal function important to infant development, even if they have no adaptive value *per se*. Therefore, the proportion of swelling during gestation may positively predict infant survival.

2.2 Methods

2.2.1 Assigning sexual swelling scores and conception dates

Records of sexual swellings in Gombe were drawn from long-term sightings records in both the A- and B-records for Kasekela females and the B-record for Mitumba females. Swellings are recorded on a fractional scale from 0 (no swelling) to 1 (full swelling) with partial swelling evaluated as 0.25, 0.5, or 0.75. Infant birthdates are typically assigned to the midpoint between the day the mother was last seen without an infant and the first day she is observed with the new infant, unless other evidence of the infant's age can be deduced. Conception dates were determined by counting back 225 days from the birthdate and identifying the most likely conceptive cycle where possible. In these cases, conception was assigned to the last day of full swelling in that cycle.

When no cycles were observed around the time of conception or when the first day of detumescence could not be established due to missing data, I employed the community average gestation length of 225 days to determine the day of conception.

Long-term records of Kanyawara females were drawn from group and focal follows. In this community, swellings are rated on a 3-point scale, where 1 is no swelling, 2 is partial swelling and 3 is fully swollen. Conception dates were assigned by Melissa Emery Thompson based on endocrine data and/or records of swelling where available, or 225 days prior to birth in all other cases. Infant date of birth was determined similarly in Kanyawara as in Gombe.

2.2.2 Defining trimesters

Each gestation was divided into three trimesters. Trimesters one and two were each 80 days, and trimester three followed from day 161 to infant birth. Because swellings are more commonly observed in the first trimester, trimester number (1, 2, 3) was included as a factor variable in all analyses that included each trimester as a separate entry.

2.2.3 Determining immigrant status

Females of known pedigree were assigned the status of “natal” if they reproduced in the community into which they had been born. In some cases, females who were alive at the start of the Gombe study but had close relationships with other adult females were presumed to be natal. Females who were observed to transfer into the study community, or between the two habituated communities at Gombe, are designated as immigrants. There remains a small number of females who were adult at the start of the Gombe study

whose immigrant status is unknown; these were coded as '2' in analyses that included immigrant status (natal = 0, immigrant = 1).

2.2.4 Calculating female dominance rank

Dominance ranks were calculated separately among females from each community using a modified Elo method. In the classic application of Elo ranking, individuals all receive identical starting positions, and their Elo scores are updated continuously based on each new dominance interaction (Elo, 1978). Foerster *et al.*, (2016) used maximum likelihood modeling to determine individuals' initial scores and the constant k , which is used to calculate the "winner's bonus" and the "loser's tax", such that these parameters best fit the dataset of observed interactions. Daily Elo scores of all adults can then be normalized relative to all other group members to generate a score between 0-1. I averaged daily normalized values within each gestation for each female. Female rank was included in all models testing the social passport hypothesis, as low-ranking females are likely to be most at risk of intrasexual aggression and therefore predicted to swell more during pregnancy in order to recruit male support and mitigate that risk. Rank was also included in survival analyses given the known relationship between female rank and reproductive success (Pusey *et al.*, 1997; Jones *et al.*, 2010).

2.2.5 Measures of post-conception swelling

Due to frequent missing observations of pregnant females, and the tendency of swellings during pregnancy to be irregular, counting a discrete number of swellings during gestation was not feasible. Therefore, I generated a variety of measures to capture the variation in swelling during gestation. For global measures of swelling within each

pregnancy, I calculated the number of days a female was observed with a full swelling relative to the number of days she was observed during her pregnancy, henceforth the proportion of observed days fully swollen. I also calculated the days observed with any swelling (full and partial swelling) and the last day in gestation that female was observed with a full swelling, counting from conception. Finally, I calculated the proportion of each trimester each female was observed fully and/or partially swollen, based on the number of days in the trimester (trimester 1 = 80 days, trimester 2 = 80 days, trimester 3 = gestation length -160).

2.2.6 Estimating cycles to conception

In the Kanyawara dataset, the number of cycles to conception was estimated for parous females as the number of months between the resumption of swelling post-partum and conception; for nulliparous females, as the number of months between onset of swelling to first conception. In the Gombe dataset, I examined each calendar month between the resumption of swelling post-partum for parous females and the onset of swellings for nulliparous females, and determined whether or not that female had been observed with a full swelling in that month. The months with full swelling were summed to generate a preliminary value for the number of cycles to conception (CTC). Because not all females are observed in every month during this window, a correction was necessary to more accurately estimate CTC. I performed a general linear mixed model with a link logit function and a binary outcome variable (swelling observed 0/1) to model the probability of observing a swelling given the time to conception (month to conception) and the quality of the observations in each month. I assumed that a swelling

could have been missed entirely when a female was observed on fewer than 20 days in a given month, since a full swelling typically lasts for 10 days (Deschner and Boesch, 2007). Because we did not ask whether the missing days were consecutive, this is a conservative estimate of our ability to observe any full swellings. Here, I also controlled for repeated observations of the same female and by including female ID as a random effect. I ran these models separately for parous and nulliparous females, because nulliparous females are likely to swell for longer intervals before their first conception, which could lead to overestimating the probability of swelling for parous females. I also included a binary variable for parous females to indicate whether the infant opening the interbirth interval had died before her next conception. These models generated predicted values for the likelihood of observing a swelling in each month prior to conception for nulliparous and parous females, respectively. I then used these model coefficients to generate the likelihood that a female had a swelling in each month by assuming that observations were always sufficient. I then substituted the predicted likelihood of having a swelling for months in which the female was not seen with a swelling and was observed on fewer than 20 days. The sum of months with observed swellings and the probabilities of swelling when observations were poor is the corrected number of cycles to conception. This variable was included in all models testing the paternity confusion hypothesis, since one of its central predictions is that females who have cycled more before conceiving are less vulnerable to infanticide and will swell less during pregnancy.

2.2.7 Data analysis

I tested for pair-wise correlations among the measures of post-conception swelling using the `cor.test` function in package `Hmisc` (Harrell, 2016). To test the hypotheses and predictions outlined in the introduction, I ran a series of linear and general linear mixed models (GLMM). All models were performed in R (R Development Core Team, 2014) using the package `lme4` (Bates *et al.*, 2014). I performed model selection using corrected Akaike information criteria (AICc) a measure of the fit of the model to the data based on maximum likelihood (Akaike, 2011) that also takes into account finite sample size (Burnham *et al.*, 2011). I present the results of all models within two points of the AICc score of the best model ($\Delta < 2$). When multiple best models were found, I performed model averaging to calculate effect sizes across all best models, where the contribution of each model is weighted according to its AICc score. Model selection and averaging were performed using the package `MuMin` (Barton, 2014). To generate predicted values based on model results for the number of cycles to conception, I used the `predictSE` function in the package `AICcmodavg` (Mazerolle, 2016). Finally, I performed a survival analysis for infants based on the amount of swelling during gestation, as well as other likely predictors. This analysis utilized Cox proportional hazards models in the R package `Survival` (Therneau and Grambsch, 2000; Therneau and Lumley, 2014; Therneau, 2015).

2.3 Results

I first present results on the correlation among measures of post-conception swellings and calculation of a corrected number of cycles to conception, as these analyses

are foundational to the following results. I then present results from the non-adaptive hypotheses as these did not receive support, before moving on to the adaptive hypotheses which will be addressed further in the discussion.

2.3.1 Correlation among measures of post-conception swelling

All measures of post-conception swelling as defined in the methods section are significantly positively correlated with each other (pair-wise Pearson’s correlations, $p < 0.001$). Measures from all pregnancies in both Gombe and Kanyawara were included in this analysis. All correlations and relevant statistics are given in Table 1 and Table 2, respectively.

Table 1: Pearson correlation between measures of post-conception swellings

	Prop full swelling (Tri 1)	Prop full swelling (Tri 2)	Prop full swelling (Tri 3)	Total prop observed fully swollen	Last day of full swelling
Prop full swelling (Tri 1)	1	0.9	0.23	0.62	0.50
Prop full swelling (Tri 2)	0.59	1	0.35	0.52	0.58
Prop full swelling (Tri 3)	0.23	0.35	1	0.27	0.46
Total prop observed fully swollen	0.62	0.52	0.27	1	0.51
Last day of full swelling	0.50	0.58	0.46	0.51	1

Table 2: Significance of Pearson correlations between measures of post-conception swellings

Measure 1	Measure 2	t	df	p
Prop full swelling (Tri 1)	Total prop observed fully swollen	10.95	193	<0.00001
Total prop obs fully swollen	Last day of full swelling	8.25	193	<0.00001
Prop full swelling (Tri 1)	Prop full swelling (Tri 2)	10.14	193	<0.00001
Prop full swelling (Tri 1)	Prop full swelling (Tri 3)	3.27	193	0.00129
Prop full swelling (Tri 2)	Prop full swelling (Tri 3)	5.26	193	<0.00001
Prop full swelling (Tri 2)	Total prop observed fully swollen	8.43	193	<0.00001
Prop full swelling (Tri 3)	Total prop observed fully swollen	3.91	193	0.00013
Prop full swelling (Tri 2)	Last day of full swelling	9.99	193	<0.00001
Prop full swelling (Tri 3)	Last day of full swelling	7.26	193	<0.00001

2.3.2 Cycles to conception

I tested for population-level differences in the waiting time to conception in Gombe and Kanyawara, based on the months between the onset or resumption of cycling and conception (months to conception, or MTC). The average MTC is 23.26 (sd =30.54, n =150) among Gombe females and 14.55 (sd = 12.19, n = 35) among Kanyawara females. This difference is significant ($t = 2.69$, $df = 139$, $p <0.01$).

As described in the methods section, I corrected for missing observations of swellings leading to conception by modeling the effect of time, in months, to conception and the quality of observations on the likelihood of observing a swelling. In pregnancies of both nulliparous (n = 46) and parous (n = 45) Gombe females, probability of observing a swelling increases as conception approaches, and decreases when observations are sparse (<20 observation days) (Table 3). In parous females, the survival of the previous infant also decreases the probability of observing a swelling in a given month prior to

subsequent conception (coefficient = -1.1119). Using these models, I generated the predicted probabilities of observing a swelling in each MTC given sufficient data (Figure 1).

Table 3: Effects of time to conception and data quality on probability of observing a swelling

Model	MTC	Insufficient Data	Infant Survives	AICc
Nulliparous	-0.0253	-0.9639	NA	1632.257
Parous	-0.0277	-3.3301	-1.1119	1591.938

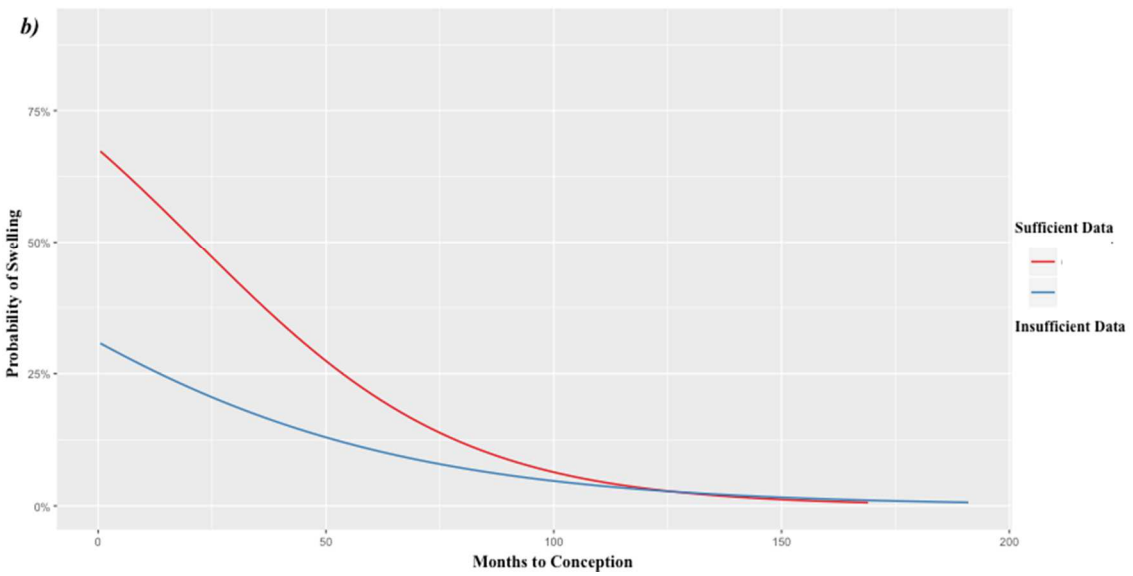
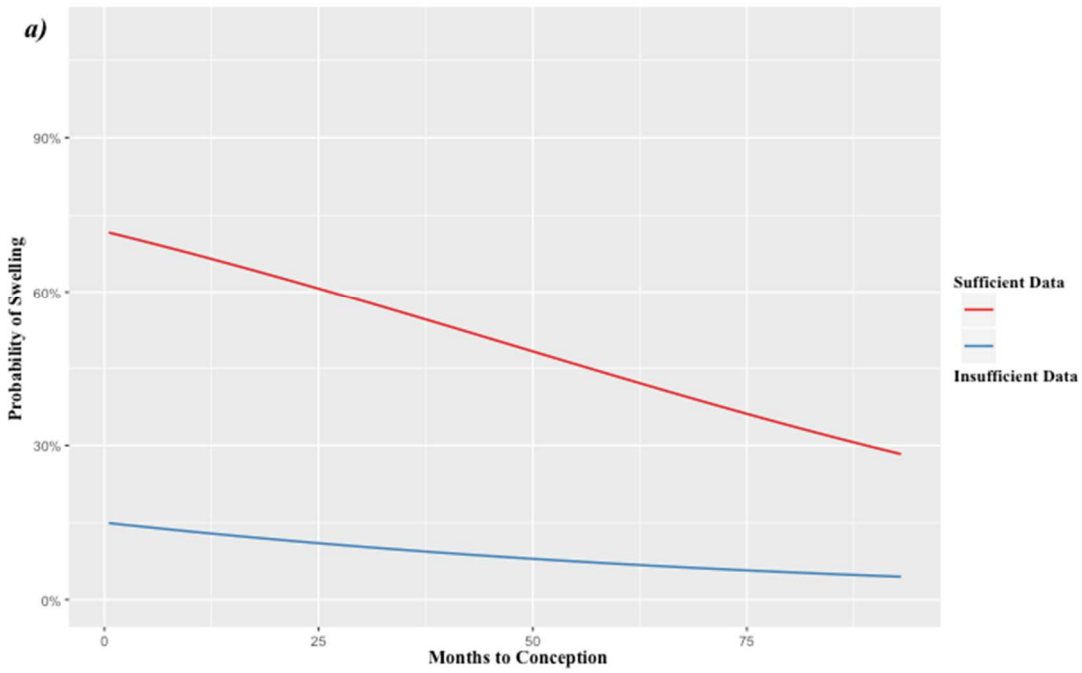


Figure 1: Predicted probability of swelling in each month to conception given sufficient or insufficient observations in that month for a) parous females and b) nulliparous females.

2.3.3 Healthy hormones hypothesis

If sexual swellings during pregnancy have no adaptive value of their own, they may still persist in spite of potential costs as a byproduct of hormone production necessary to maintain a pregnancy to full term. Following the predictions outlined in the introduction, I first tested whether the trimester of pregnancy (1, 2, or 3) was the primary predictor of the proportion of time fully swollen. I ran a LMM with the continuous outcome variable of proportion of each trimester fully swollen, excluding all trimesters where the female was observed on less than 25% of the trimester ($n = 293$ trimesters, 140 pregnancies, 62 females). This analysis included females from Kanyawara, Kasekela, and Mitumba. Other fixed effects were mother's age at birth, mother's average rank during gestation, mother's immigrant status, and mother's cycles to conception. I included random effects for female ID and pregnancy ID to account for repeated measures in these variables. In the full model, age showed a trend toward a negative effect ($p = 0.0547$) on proportion of full swelling, immigrant status showed a trend toward a positive effect ($p = 0.0529$), and trimesters two and three each had strong negative effects on proportion of swelling relative to trimester one ($p < 0.0001$). Model selection based on AICc yielded a single best model including only the fixed effect of trimesters 2 and 3 as predictors (Table 4). This result supports the prediction that the typical progression of hormone production is predictive of swelling in early pregnancy (Figure 2).

Table 4: Factors influencing proportion of each trimester fully swollen

Model	CTC	Avg Elo	Imm	F ID	Preg ID	Tri 2	Tri 3	AICc
1						-0.0453	-0.1161	569.96

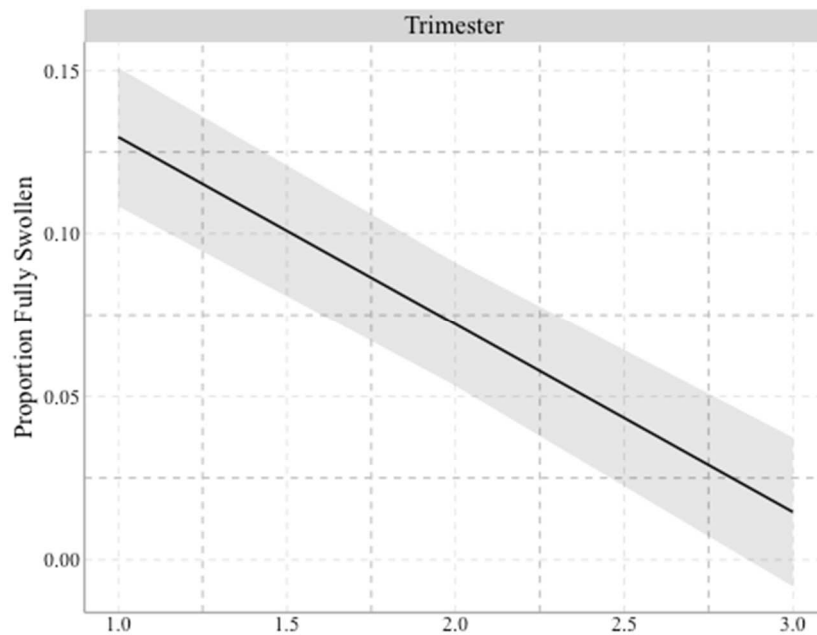


Figure 2: Marginal effect of advancing trimester (1, 2, or 3) on the proportion of full swelling in each trimester. Shaded area represents the 95% confidence interval of the effect.

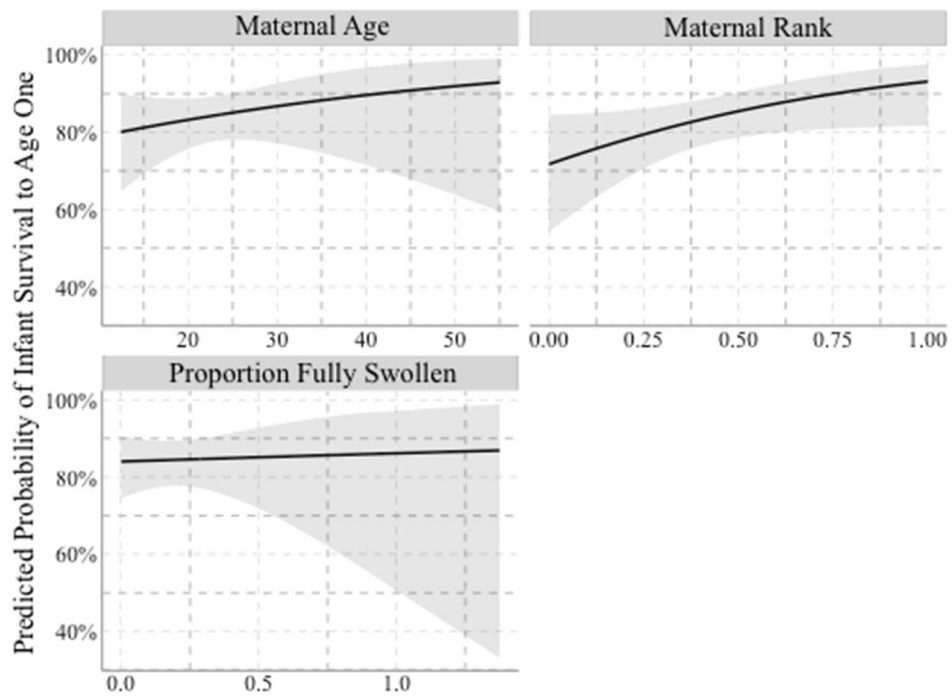
Next, I tested whether the amount of swelling in pregnancy, measured by either the last day of full swelling or the proportion of observed days fully swollen, predicted infant survival to age one in females from Kanyawara and Gombe using GLMMs with a binary outcome variable of survival to age one and a logit function. Model selection based on AICc yielded two best models including mother’s age and mother’s rank. Neither last day of full swelling nor proportion of observed days fully swollen appeared in the best models, nor were they significant predictors in the full model (Table 5, Table 6). Marginal effects of maternal age, rank, last day of full swelling, and the proportion of observed days with full swelling are illustrated in Figure 3.

Table 5: Factors influencing infant survival to age one

Model	Age	Avg Elo	Imm	Last Day Full Swelling	AICc	Delta	Weight
1		1.979			158.4731		0.6460
2	0.0300	1.6410			159.6764	1.2033	0.3540
Average	0.0300	1.8594					

Table 6: Factors influencing infant survival to age one

Model	Age	Avg Elo	Imm	Prop Obs Full Swelling	AICc	Delta	Weight
1		1.979			158.4731		0.6460
2	0.0300	1.6410			159.6764	1.2033	0.3540
Average	0.0300	1.8594					



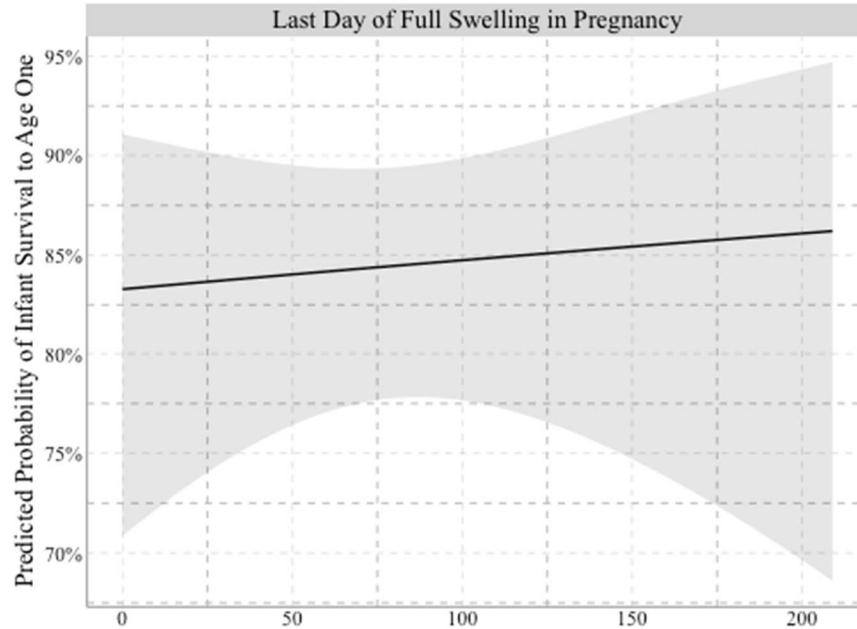


Figure 3: Effects on infant survival to age one. Predicted probabilities for survival are drawn from the full models. Top panels, clockwise from top left: Maternal age (years), maternal rank (average normalized Elo score), proportion of pregnancy observed with a full swelling. Bottom panel: Effect of last day of full swelling on infant survival to one. Shaded area indicated 95% confidence interval.

I also ran a Cox proportional hazards model among Gombe infants for whom I had dates of death ($n = 140$ infants). Neither the last day of full swelling nor total proportion of observed days with a full swelling significantly predicted infant survival to age two ($n = 38$ deaths) or five ($n = 53$ deaths). Again, mother's rank at birth was the only significant predictor of infant survival. Given the consensus among these models and the GLMMs presented above, I did not perform model selection but instead present results from each full Cox model (Table 7, Table 8, Table 9, Table 10). Because Cox models estimate the hazard of death, maternal rank has a negative coefficient, but this represents the same effect of improved infant survival among higher-ranking females.

Table 7: Factors influencing hazard of infant death before age two in Gombe

	Maternal Age	Maternal Rank	Immigrant	Prop Obs Full Swelling
coefficient	0.0235	-1.5539	-0.1315	0.3149
p-value	0.39	0.041*	0.64	0.76

Table 8: Factors influencing hazard of infant death before age two in Gombe

	Maternal Age	Maternal Rank	Immigrant	Last Day Full Swelling
coefficient	0.0254	-1.5508	-0.1395	0.0014
p-value	0.36	0.039*	0.62	0.65

Table 9: Factors influencing hazard of infant death before age five in Gombe

	Maternal Age	Maternal Rank	Immigrant	Prop Obs Full Swelling
coefficient	0.0267	-1.5883	0.0299	-0.3583
p-value	0.26	0.013*	0.9	0.7

Table 10: Factors influencing hazard of infant death before age five in Gombe

	Maternal Age	Maternal Rank	Immigrant	Last Day Full Swelling
coefficient	0.0263	-1.5610	0.0254	-0.0006
p-value	0.27	0.014*	0.91	0.81

2.3.4 Seasonality and energetic constraints

Energy availability is linked to reproductive hormone production and function (Emery Thompson et al., 2010, 2012; Emery Thompson, 2013), and seasonal effects on cycling and conception have been reported in Gombe (Wallis, 1995). I tested the hypothesis that pregnant females will swell more during the late dry and early wet

seasons by modeling the effects of the proportion of gestation spent in each of four seasons on the proportion of observed days with full swelling during pregnancy. In support of this prediction, the proportion of gestation that falls in the early dry season is inversely related to the proportion of observed days with full swelling (coefficient = -0.3454). Although maternal age was a significant predictor in the full model ($p = 0.005$), the single best model based on AICc criteria includes only the proportion of gestation in the early dry season (Table 11).

Table 11: Seasonal effects on the proportion of observed days with full swelling

Model	Age	Prop Early Wet	Prop Late Wet	Prop Early Dry	Prop Late Dry	AICc
1				-0.3454		-58.1025

2.3.5 Paternity confusion and social passport hypotheses

In order to promote the social benefits proposed in these adaptive hypotheses, post-conception swellings must have the effect of increasing female association with males. To demonstrate this trend, I tested the effect of the proportion of observed days with full swelling on the sum of dyadic associations (DAI strength) with male partners for a subset of Gombe females for whom these data were available ($n = 46$ pregnancies in 21 females; see chapter two for details on calculation of DAI values and criteria for inclusion). The proportion of observed days fully swollen appears in four of six best models as a positive predictor of total DAI strength during pregnancy, even when controlling for other likely predictors of female sociality (Table 12). Immigrant status is

coded as 0 for natal females, the reference category, and 1 for immigrant females;

marginal effects of all predictor variables are illustrated in Figure 4.

Table 12: Effect of proportion of observed days fully swollen on association with males

Model	Age	Average Elo	Immigrant Status	Prop Obs Fully Sw	AICc	Delta	Weight
1		-0.9262	-1.3532	1.9364	199.8974		0.2640
2			-1.213	2.317	199.9698	0.0724	0.2546
3				1.398	201.3102	1.4128	0.1303
4		-1.177	-1.239		201.3581	1.4607	0.1272
5		-0.299		1.182	201.3581	1.4607	0.1235
6			-1.035		201.4158	1.5184	0.1005
Average		-0.8376	-1.2432	1.8502	201.8294	1.932	

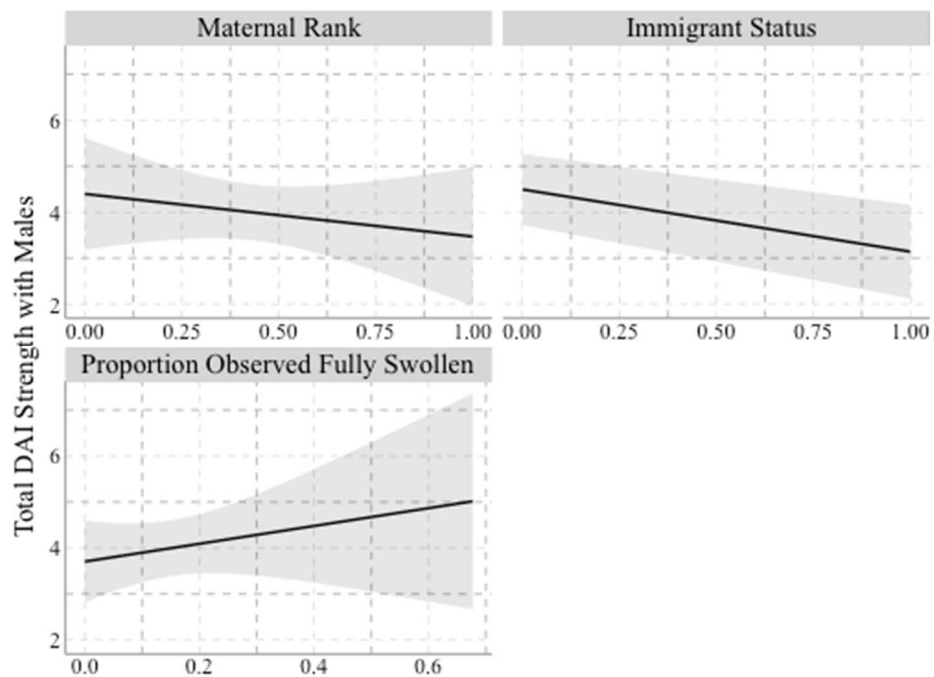


Figure 4: Marginal effects on females' total DAI strength with male partners. Clockwise from top left: Maternal rank (average normalized Elo score), immigrant status (0 = natal, 1 = immigrant), and proportion of observed days fully swollen.

Predicted DAI strengths are drawn from the top model based on AICc. Shaded areas indicate 95% confidence interval.

I then tested the two adaptive hypotheses outlined in the introduction together, by including the predicted effects for both hypotheses in linear mixed models with last day of full swelling as the outcome variable. The key predictors for the paternity confusion hypothesis are age, cycles to conception, and immigrant status. Immigrant status and female rank are the major predictors in the social passport hypothesis.

Among Gombe females (n = 122 pregnancies in 42 females), model selection yielded two best models. In the average model, females who cycled more before conceiving stopped swelling earlier in pregnancy (coefficient = -0.13), as did higher-ranking (coefficient = -35.66) and older (coefficient = -2.25) females. Immigrant females were more likely to swell later into gestation (coefficient = 24.96). These results all follow the predictions of both the paternity confusion and social passport hypotheses. Best models are summarized in Table 13; marginal effects are illustrated in Figure 5.

Table 13: Factors influencing the last day of full swelling among Gombe females

Model	Corrected CTC	Avg Elo	Age	Immigrant	AICc	Delta	Weight
1		-35.6	-2.246	24.845	1290.921		0.7006
2	-0.1343	-35.7865	-2.2521	25.2259	1292.622	1.701	0.2993
Average	-0.1343	-35.6558	-2.2480	24.9593			

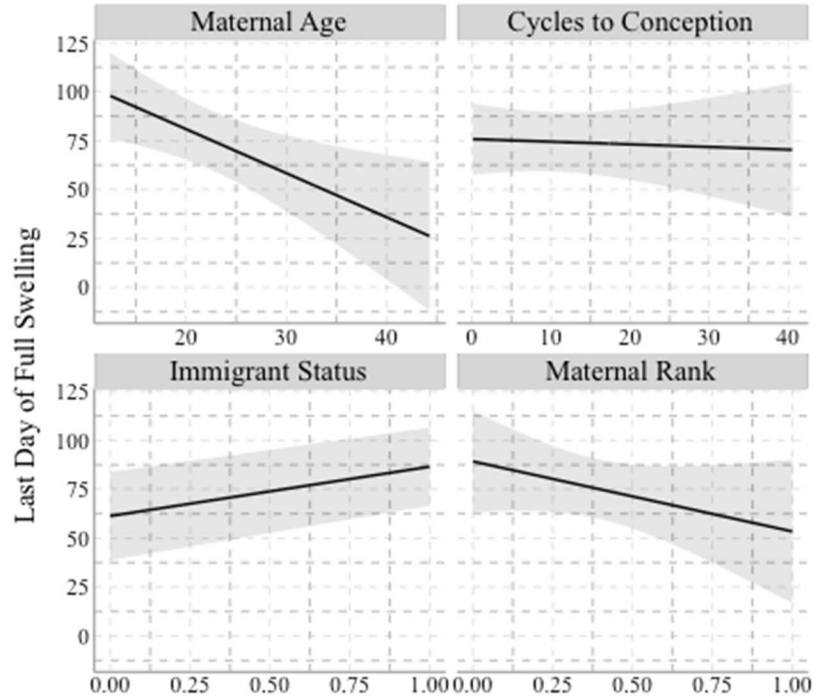


Figure 5: Marginal effects on the last day of full swelling in Gombe females. Clockwise from top left: Maternal age (years), number cycles to conception, maternal rank (average normalized Elo score), and immigrant status (0 = natal, 1 = immigrant). Predicted values are drawn from model 2, Table 12. Shaded areas indicate 95% confidence intervals.

Among Kanyawara females ($n = 33$ pregnancies in 16 females), model selection also yielded two best models (Table 14). As in Gombe, older females (average coefficient = -2.7) stopped swelling sooner. However, some predictors showed opposite effects to those found in Gombe. Females with longer waiting times to conception, measured as months from onset of swelling to conception, continued to swell later into gestation (average coefficient = 0.21). Higher-ranking females had full swellings later in gestation (average coefficient = 46.54), while immigrant (average coefficient = -2.37) females stopped cycling sooner. Marginal effects are illustrated in Figure 6.

Table 14: Factors influencing the last day of full swelling among Kanyawara females

Model	Months to Conception	Maternal Rank	Age	Immigrant	AICc	Delta	Weight
1		44.568	-2.705	-2.633	342.4172		0.6637
2	0.214	50.429	-2.69	-1.864	343.7771	1.3599	0.3363
Average	0.2140	46.5389	-2.7001	-2.3740			

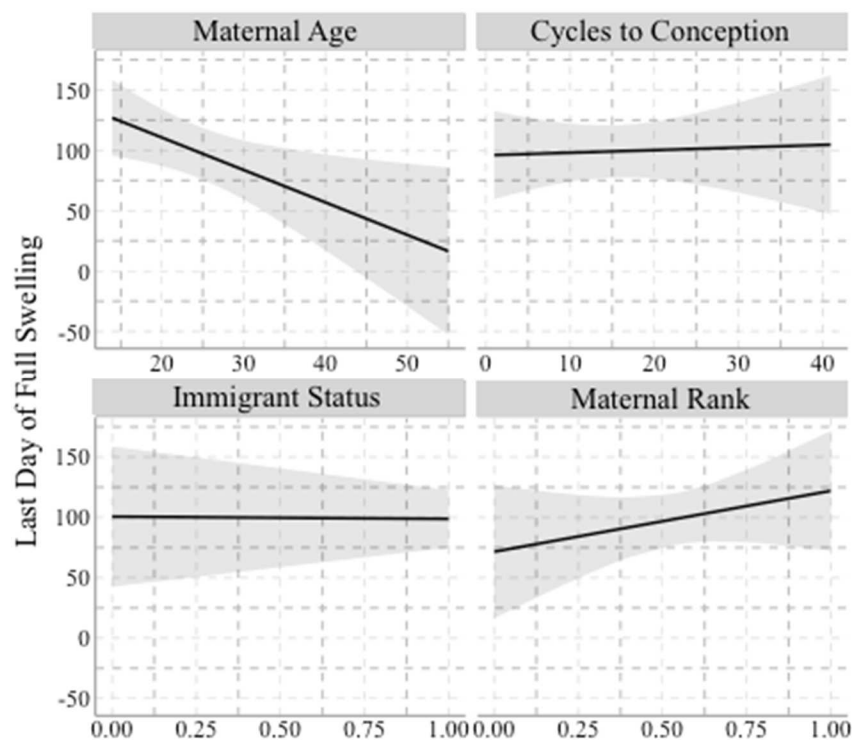


Figure 6: Marginal effects on the last day of full swelling in pregnancy among Kanyawara females. Clockwise from top left: Maternal age (years), number of cycles to conception, maternal rank (average normalized Elo score), and immigrant status (0 = natal, 1 = immigrant). Predicted values are drawn from model 2, above. Shaded areas indicate 95% confidence intervals.

In the Kasekela community at Gombe, approximately half of all females remain in their natal communities throughout their lives; in Kanyawara, only three females have been observed to do so. Therefore, the composition of resident females varies

considerably between these two populations, and may explain the opposite direction of the effect of immigrant status on post-conception swellings. To avoid this confound, I combined immigrants from Gombe and Kanyawara to examine the effects of cycles to conception, rank, and age on the last day of full swelling. I also included a factor variable for community to test for group-level effects (Table 15). Among immigrants, older (average coefficient = -2.76) and higher-ranking (average coefficient = -7.62) individuals stop swelling earlier in gestation. Cycles to conception (corrected for Gombe females, MTC for Kanyawara females) slightly positively predict the last full day of swelling in pregnancy (average coefficient = 0.01). Overall, immigrants in Kanyawara swell later into gestation than do Kasekela females (average coefficient = 15.62); Mitumba females swell later into gestation than do Kasekela females (average coefficient = 7.73).

Table 15: Factors influencing the last day of full swelling in Gombe and Kanyawara Immigrants

Model	CTC	Maternal Rank	Maternal Age	Community (KW)	Community (MT)	AICc	Delta	Weight
1		-7.641	-2.763	15.637	7.735	1061.63		0.7120
2	0.0104	-7.5563	-2.7644	15.5743	7.7126	1063.44	1.81	0.2880
Average	0.0104	-7.6164	-2.7637	15.6189	7.7285			

For Gombe immigrants, I also examined the effect of tenure, measured in years, in the adult community prior to conception in the first pregnancy as a predictor of the last day of full swelling (n = 21 primipara). The paternity confusion hypothesis predicts that recent immigrants who have had less time to mate with all community males will swell more in pregnancy to compensate; these females are also likely the most vulnerable to female aggression and in need of male support. As predicted by both adaptive

hypotheses, more recent immigrants continue to swell longer into gestation during their first pregnancies in their adult communities, yielding a negative correlation between tenure length and the last day of full swelling (average coefficient = -2.9674). Results are summarized in Table 16, and marginal effects are illustrated in Figure 7.

Table 16: Factors influencing the last full day of swelling in first births among Gombe immigrants

Model	CTC	Maternal Rank	Age	Tenure	AICc	Delta	Weight
1				-3.003	1511.898	0	0.4430
2		-11.721		-2.831	1513.546	1.648	0.3845
3	-0.2056			-3.0324	1513.855	1.957	0.1725
Average	-0.2056	-11.7206		-2.9674			

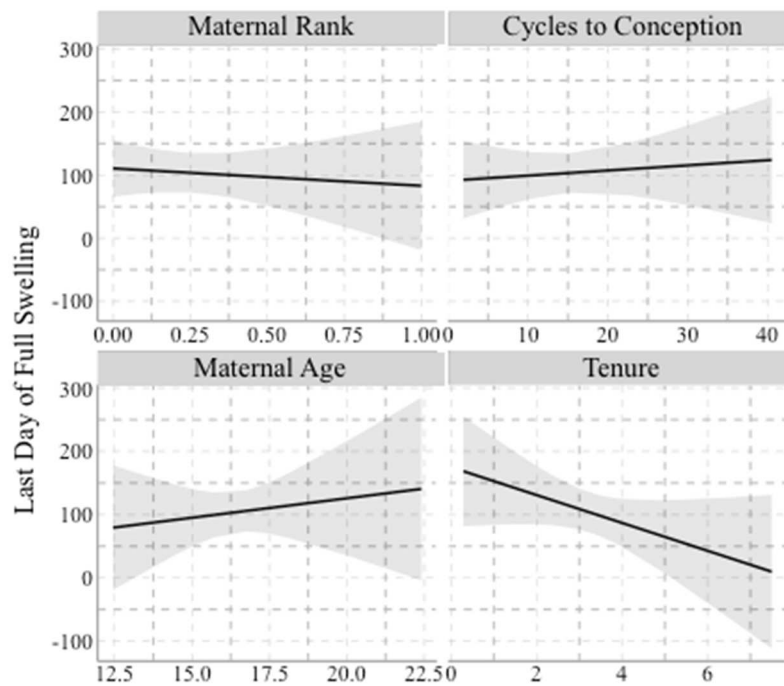


Figure 7: Marginal effects on the last day of full swelling in first pregnancy in Gombe immigrants. Clockwise from top left: Maternal rank (average normalized Elo score), number of cycles to conception, immigrant tenure before conception

(years), and maternal age at birth (years). Predicted values are drawn from the full model. Shaded areas indicate 95% confidence intervals

2.4 Discussion

2.4.1 Evaluating the paternity confusion hypothesis

Here, I demonstrated that pregnant females who swell more also have stronger associations with males during gestation. In Kanyawara, estrous, cycling females spend more time within five m of males than do anestrus females, and also receive more grooming from males (Machanda et al., 2013), a pattern that is likely to be similar in Gombe. While not surprising, these findings together validate the assumption that cycling during pregnancy can increase females' access to males and the benefits that may accrue as a result.

One of these benefits is the opportunity to mate. In Kanyawara, females conceive more quickly after the onset of cycling, leading to shorter windows of sexual receptivity relative to Gombe females. They also exhibit more post-conception swellings than do females in both communities at Gombe. Among Gombe females, the number of cycles leading to conception is inversely related to the proportion of pregnancy observed with a full swelling, such that females that have cycled less before conceiving swell more after. These inter-population and inter-individual differences suggest that post-conception swellings offer an opportunity to compensate for short periods of sexual receptivity and more thoroughly confuse paternity. Such flexibility has been observed in other species as an infanticide avoidance strategy: In one study of red colobus monkeys, pregnant resident females mated with an infanticidal male only when they had not done so before conceiving (Struhsaker and Leland, 1985).

External factors may restrict females' ability to mate widely before conception. Adult males prefer mating with older, parous females, likely due to their proven value as reproductive partners (Muller et al., 2006). Younger, less attractive females may require more time and effort to achieve paternity confusion. In this study, female age had the strongest and most consistent effect on the amount of post-conception swelling: older females swell less during pregnancy. Physiological factors may also underlie this pattern: in both chimpanzees and bonobos, younger females have been shown to be more sensitive to the effects of estrogen, exhibiting full tumescence in response to absolutely lower levels of the hormone (Dahl et al., 1991). This sensitivity may be advantageous, allowing young females to exploit additional opportunities to mate even during low-fertility periods.

Immigrant females may be more vulnerable to infanticide, given their lack of adult relatives within the community, and shorter mating histories with resident males. In Gombe, where approximately 50% of females remain in their natal communities, immigrants swell significantly more during pregnancy than do natal females. The tenure of an immigrant female in her adult community seems to matter, as well. Community tenure before first birth—in a very literal sense, a measure of females' opportunity to mate with with resident males—is inversely related to the last day of full swelling during pregnancy, even when controlling for age, rank, and the number cycles to conception. This finding upholds the predicted relationship between pre-conception cycles and post-conception swelling.

In spite of the evidence presented above, some findings in this study do not support the paternity confusion hypothesis. Among Kanyawara females, immigrants cycle less than do natal females. However, the sample from this population includes only three pregnancies in two natal females. In all three, swelling persisted relatively late into gestation (105-162 days). Furthermore, I found a positive correlation between pre- and post-conception cycling in both Kanyawara and the sample of immigrants from both populations. However, it should be noted that I was unable to perform the same predictive modeling of cycles to conception in the Kanyawara sample, and instead used only the number of months between the onset of cycles and conception. This may have lead to an overestimate of the cycles to conception in Kanyawara, which could affect the relationship between the two periods of sexual receptivity.

2.4.2 Evaluating the social passport hypothesis

Mating opportunities and paternity confusion are likely not the only benefits of male-female association during pregnancy. Females that swell more during pregnancy, shown here to associate more with males during this time, may also receive protection against aggression from other females. The effects of rank on the extent of post-conception swelling demonstrated in this study support this hypothesis. Low-ranking females are more vulnerable to intrasexual aggression (Pusey and Schroepfer-Walker, 2013), and, in Gombe, swell more during pregnancy than do high-ranking females. Resident females can be extremely hostile and aggressive toward immigrants (Watts, 1992; Kahlenberg et al., 2008b; Pusey et al., 2008), and in Gombe, immigrants are more likely to swell during pregnancy. Among immigrants in both populations, those that are

higher-ranking, likely those with longer community tenure, stop swelling earlier in gestation. As discussed above, the most recent immigrants spend a greater proportion of their first gestations with full swellings.

Again, findings from Kanyawara do not consistently align with predictions for this adaptive hypothesis: immigrants swell less than do natal females, but the same caveats to this result apply here. Among all Kanyawara females, higher-ranking females are in fact more likely to swell later into gestation. This effect disappears when looking only among Kanyawara immigrants. The few natal females included in the Kanyawara sample were high-ranking and also swelled late into gestation, and may explain the overall positive correlation between rank and last day of full swelling.

2.4.3 Evaluating the healthy hormones hypothesis

When trimesters are considered individually, while controlling for both female and pregnancy ID, trimester number (first, second, or third trimester) was the strongest predictor of the proportion of full swelling. More swelling occurs in first trimesters than in second or third. This suggests a strong physiological effect of typical hormone production during pregnancy on the ability of females to mount a full swelling (Wallis and Goodall, 1993; Shimizu et al., 2003). Across primate species, swellings are more common early in pregnancy than late (Gordon et al., 1991; Gust, 1994; Möhle et al., 2005), and this has been documented in captive chimpanzees, as well (Dahl, 1999). However, swellings do persist into the later trimesters in many females in this sample, indicating that hormonal control does not strictly inhibit swellings later in gestation.

However, the critical component of the healthy hormones hypothesis is the prediction that swellings represent hormone activity necessary for a successful pregnancy. Instead, I found no effect of swelling in pregnancy on infant survival to age one in both populations. Upon further investigation among Gombe births, I also found no effect of swelling on infant survival to ages two and five. In fact, the only significant predictor of infant survival was maternal rank at birth, which is negatively associated with the amount of full swelling during pregnancy. Improved survival in infants of high-ranking mothers has been documented in chimpanzees (Pusey et al., 1997) and in baboons (Silk et al., 2003; Wasser et al., 2004). The many successful, completely detumescent pregnancies observed in the wild suggest that the pathological outcomes observed in captive studies (Dahl, 1999) may be more attributable to maternal distress in a laboratory setting than to physiological dysfunction.

2.4.4 Evaluating the energetic constraints hypothesis

I found a seasonal effect on the proportion of time fully swollen during gestation that aligns with food availability in Gombe and supports the energetic constraints hypothesis (Pusey et al., 2005). Pregnancies that span the early dry season showed a lower proportion of observed days with full swelling; this is a time with low food availability (Wallis, 1995). Given that cycling females may cease to swell during these seasons of food stress, it is not surprising that pregnant females may also experience a reduction in swellings. Similar effects have been documented in yellow baboons, swelling size in this species typically increases with successive cycles leading to

conception, but these increases were suppressed during a period of drought (Fitzpatrick et al., 2014).

Due to failure of sample preservation, I was unable to measure c-peptide concentrations among pregnant females and therefore relied on proxies for energetic condition to test this hypothesis. High-ranking females may have improved access to resources due to their enhanced competitive ability (Emery Thompson et al., 2007; Murray et al., 2007a; Kahlenberg et al., 2008a). They are therefore expected to swell more during pregnancy according to the energetic constraints hypothesis, but my data show that they are in fact less likely to swell during pregnancy. Recent immigrant females, likely to lack familiarity with food sources within their new community ranges, and to face aggressive exclusion from high-quality patches (Miller et al., 2013), are more likely to swell during pregnancies. This finding also contradicts the energetic constraints hypothesis. While all females are likely subject to environmental effects on their reproductive function, an energetic hypothesis is a poor explanation for between-female variation in post-conception swellings.

2.4.5 Other potential explanations: The cost-of-sexual-attraction hypothesis

Wrangham (2002) proposed the cost-of-sexual-attraction hypothesis to explain inter-population differences in the number of cycles to conception. He argued that females in permissive environments are better able to buffer the loss of foraging efficiency and increased travel imposed by estrus swellings. Therefore, they should cycle more in order to decrease the value of each cycle from the male perspective, thereby reducing the amount of sexual coercion that they receive. This effect has been demonstrated in red

colobus monkeys (*Procolobus rufomitratu*s): Relative to females in old-growth forests, females in logged forests, which represent a degraded, lower-quality habitat, had shorter phases of full tumescence. During full tumescence, they mated at higher frequencies, and sexual behaviors were restricted to this phase, while old-growth forest females also mated while partially tumescent or flat (Milich et al., 2014). Within chimpanzee communities, older, high-ranking females have improved access to resources. They may therefore be expected to use this strategy, possibly extending it into gestation. However, I have demonstrated that females who are potentially more energetically stressed, due to low social rank and recent immigration, are those more likely to exhibit post-conception swellings. Therefore, I can conclude the cost-of-sexual-attraction hypothesis cannot explain the patterns of post-conception swelling in Gombe. Instead, the findings presented here support the conclusion that post-conception swellings in chimpanzees function to confuse paternity and reduce the risk of infanticide for those females who are most vulnerable to this threat. Because infanticide is observed rarely, collaboration across field sites will be necessary to test whether females who swell during pregnancy are in fact less likely to lose infants to infanticidal males. Intrasexual aggression may also create selective pressure on low-ranking females to swell during pregnancy and elicit support from males. Future work should determine whether males are more likely to intervene on behalf of females who swell more during pregnancy.

3. Promiscuity or Partner Preference? Male-Female Interactions Across Reproductive States Reflect Female Strategies for Avoiding Aggression

3.1 Introduction

Anthropoid primates are generally characterized by permanent social groups consisting of both males and females (van Schaik and Kappeler, 1997). These year-round associations create opportunities for both cooperation and conflict between the sexes, and strategies for optimizing intersexual relationships may evolve in response to these pressures. In chimpanzees (*Pan troglodytes*), fission-fusion social organization allows for individuals to be flexible in their overall sociality as well as in their preferences for particular social partners (Goodall, 1986; Matsumoto-Oda, 1999a; Otali and Gilchrist, 2006; Wakefield, 2013). These preferences are likely to shift in female chimpanzees as they transition between reproductive states, as they must optimize mating and grooming relationships with aggression avoidance.

Female chimpanzees are less gregarious than males and spend more time foraging alone or with only their dependent offspring (Wrangham and Smuts, 1980; Mitani et al., 2002; Otali and Gilchrist, 2006; Gilby and Wrangham, 2008; Wittiger and Boesch, 2013). This may be to avoid feeding competition and reduce time spent traveling, both correlates of increased party size (Wrangham et al., 1993; Janson and Goldsmith, 1995; Matsumoto-Oda, 1998; Matsumoto-Oda and Oda, 2001). While females generally spend less time in large parties than do males, female behavior is strongly influenced by reproductive state. Each ovarian cycle lasts approximately 33-34 days on average, with full swelling for an average of 12-13 days; cycles tend to be longer in nulliparous than

parous females, and vary among populations (Wallis, 1997; Deschner et al., 2003; Matsumoto-Oda et al., 2007; Emery Thompson, 2013). Females may cycle for a period of months or years before conceiving; pregnancy lasts an average of 225 days (Boehm and Pusey, in prep), and the average interbirth interval at Gombe is approximately five and a half years when offspring survive. There are distinct costs and benefits to sociality during each of these stages.

3.1.1 Costs to estrous females and the risk of infanticide

Estrous females are more gregarious than their anestrus, lactating, and pregnant counterparts. Swollen females increase party size in two ways: They tend to join parties with high-ranking males, and attract lower-ranking males to these parties (Matsumoto-Oda, 1999a). Thus, parties are larger on days when fully swollen females are mating (Georgiev et al., 2014). However, participation in large parties imposes energetic and social costs. The number of males a female associates with in a given month negatively predicts her c-peptide level, a biomarker of energy availability (Emery Thompson et al., 2014). Furthermore, cycling, fully swollen females have the lowest c-peptide levels, when compared to cycling, non-swollen females and those in early lactation (Emery Thompson et al., 2014). Estrous females are active for longer daily periods than non-swollen females (Lodwick et al., 2004). Males, too, suffer reduced foraging while engaging in mate-guarding: male-female associations may be costly for all involved (Georgiev et al., 2014). Estrous females also receive more aggression from males in the form of sexual coercion (Smuts and Smuts, 1993; Muller et al., 2007, 2009, 2011). Even anestrus females can be the targets of sexual aggression: aggression toward cycling,

non-swollen females improves males' odds of siring subsequent offspring (Feldblum et al., 2014).

Mothers, in particular, may avoid large parties to reduce the risk of infanticide (Takahata, 1985; Arcadi and Wrangham, 1999; Paul et al., 2000; Otali and Gilchrist, 2006). Infanticide by community males is well established as an effective male reproductive strategy when likelihood of paternity is concentrated in one male and when the death of an infant will improve and accelerate the infanticidal male's likelihood of mating with the mother (Hrdy, 1979; van Schaik, 2000). In spite of promiscuous mating and low paternity certainty in chimpanzees, males have been responsible for the deaths of several community infants at Gombe and other sites, often targeting the infant while leaving the mother unharmed (Takahata, 1985; Murray et al., 2007b; Wilson et al., 2014). One Kasekela female has lost her last two infants to infanticide by the alpha male, after having conceived each on consortship with other, lower-ranking males, indicating that males may be able to track mating history and estimate their own likelihood of paternity of individual infants (Mjungu et al., 2014). Females also risk infanticide by other females, an extreme manifestation of intrasexual competition; infanticidal females are most likely to kill newborns under the age of two months (reviewed in Pusey and Schroepfer-Walker, 2013). Less extreme intrasexual aggression can also be costly for females, and tends to be directed at young, low-ranking, or recently immigrated individuals (Kahlenberg et al., 2008a; Pusey et al., 2008). Harassment of sexually receptive females by other females has been reported in other multi-male, multi-female

primates, and may be a strategy for reproductive suppression of competitors (yellow baboons, Wasser and Starling, 1988; chacma baboons, Huchard and Cowlshaw, 2011).

3.1.2 Benefits of sociality and strategies for avoiding aggression

Sociality is not without benefit for female primates: and some of these benefits involve counterstrategies to infanticide. Females can confuse paternity by mating with a large number of males. In chimpanzees, exaggerated sexual swellings provide females with a long receptive window relative to the periovulatory period (Hrdy, 1979; Dixson, 1983; Goodall, 1986; Deschner et al., 2003; Emery Thompson, 2005). According to the graded signal hypothesis (Nunn, 1999), subtle cues of maximum fertility within the swelling allows a female to mate with the most preferred males during the most fertile days while mating promiscuously earlier in her swelling. Males may be preferred on the basis of dominance rank, body condition, or other signals of high quality. This hypothesis is supported by mating patterns, where alpha males are most likely to mate toward the end of maximal swelling (Deschner et al., 2004; Stumpf and Boesch, 2005, 2006; Emery Thompson and Wrangham, 2008).

In addition to distributing likelihood of paternity, females may gain male support against intrasexual aggression when they participate in parties. Males support new immigrant females in intrasexual aggression (Kahlenberg et al., 2008b), and often intervene in disputes among resident females, sometimes during infanticidal attempts (Sterck et al., 1997; Pusey and Schroepfer-Walker, 2013). If this is the case, females would benefit most from associating with the males most likely to provide protection from infanticidal females or males: male kin, sires, and high-ranking males.

3.1.3 Kin recognition and paternal care in primates

True paternal care is rare among mammals and not expected to occur in multi-male, multi-female systems with promiscuous mating where paternity certainty is low. Nevertheless, recognition of paternal kin, including sires, has been reported in a variety of non-monogamous primate species, in the form of preferential association (Charpentier et al., 2007; Langos et al., 2013) and inbreeding avoidance (Muniz et al., 2006). Friendships in chacma baboons (*Papio hamadryas ursinus*) are most likely to form between mothers of new offspring and the males with whom they spent the greatest proportion of their fertile window in an exclusive mating association; that is, with the most likely sires, who offer protection against infanticide attempts from new immigrant males (Palombit, 2009; Moscovice et al., 2010). In yellow baboons (*P. cynocephalus*), males preferentially intervene on behalf of their genetic offspring in agonistic encounters (Buchan et al., 2003), and the presence of fathers during infancy and juvenility accelerates reproductive maturation in both male and female offspring (Charpentier et al., 2008). Male desert baboons (*P. ursinus*) may help their genetic offspring gain access to higher-quality food resources by associating preferentially with them during foraging (Huchard et al., 2012). Together, these findings suggest that paternal care can exist in a promiscuous mating system and can provide fitness benefits to offspring and sires.

Here, I examine dyadic associations between females and males before, during, and after pregnancies. I tested the alternative hypotheses that females associate, mate, and groom promiscuously, thereby confusing paternity, or that females concentrate their

social relationships on one or a small number of males who are likely and able to act as protectors after the offspring is born.

3.1.4 The promiscuity hypothesis

Paternity confusion as a mechanism for infanticide avoidance is a well documented explanation for promiscuous mating behavior in multi-male, multi-female social systems (Struhsaker and Leland, 1985; Deschner, 2000; van Schaik, 2000; van Schaik et al., 2000; Palombit, 2015). Male-female dyadic associations and interactions across reproductive states may be a result of this female strategy: According to this hypothesis, females should associate widely and with as many males as possible, both before and during pregnancy, to confuse paternity and avoid infanticide and male aggression after pregnancy; male aggression may be directly toward infants or indirectly, toward the mother. This hypothesis yields several predictions. First, dyadic rates of association, mating, and grooming before pregnancy will be inversely related to rates during pregnancy as females attempt to strengthen relationships that they failed to develop before conception, to mediate the risk of infanticide from these males. Therefore, I tested whether the strength of these measures within dyads before pregnancy is negatively correlated to the strength of association during and after pregnancy. Second, grooming, association, and mating will not be skewed heavily toward any one male partner in each period, and will be spread among all potential male partners. To examine this prediction, I asked whether particular male traits, such as dominance rank, age, sire status, and relatedness, strongly predicted associations within each period; this hypothesis predicts a random distribution of associations with respect to male traits. And third,

females with the greatest number of association, grooming, and mating partners before and during pregnancy, rather than the strongest associations, will receive less aggression after pregnancy. I tested the effects of the number and strength of associations with male partners on aggression received. I also calculated the evenness of females' associations with their male partners to test whether females with less skewed relationships also received less aggression.

3.1.5 The protection hypothesis

Males can intervene on behalf of females in intrasexual aggression or during attacks by other males (Kahlenberg et al., 2008b). Females may gain protection from particular males, such as the sire of their infants, by creating strong associations, grooming bonds, and mating histories with these males. If this hypothesis is correct, I predict that, during pregnancy, females will continue to associate, groom, and mate more with males with whom they had the strongest relationships before pregnancy. Therefore, I tested whether rates of these behaviors within dyads were positively correlated across periods. The hypothesis also predicts that grooming and association should be skewed heavily toward male partners who are likely and able to provide protection, such as sires, closely related males, and high-ranking males; sires and high-ranking males are also likely to be frequent mating partners. I tested whether these male traits were predictive of the strength of dyadic associations within periods. Finally, according to this hypothesis, strength, rather than number, of male relationships before and during pregnancy will be predictive of reduced aggression after pregnancy. I asked whether females with strong

associations received less aggression in the year after birth. Table 17, below, summarizes these questions and the predicted effects for both hypotheses.

Table 17: Summary of questions and predictions

Question	Hypothesis 1: Promiscuity and Paternity Confusion	Hypothesis 2: Protection
Association: Who do females spend the most time with?	<i>Before conception:</i> All males; not biased based on male characteristics <i>During pregnancy:</i> Biased toward males with previously weak associations <i>After birth:</i> Biased toward males with previously weak associations	<i>Before conception:</i> Biased toward sires, high-ranking, and related males (protectors) <i>During pregnancy:</i> Biased toward protectors, previously strong partners <i>After birth:</i> Biased toward protectors, previously strong partners
Grooming: Who do females groom most with?	<i>Before:</i> All males; not biased based on male characteristics <i>During:</i> Biased toward males with previously weak associations <i>After:</i> Biased toward males with previously weak associations	<i>Before:</i> Biased toward sires, high-ranking, and related males (protectors) <i>During:</i> Biased toward protectors and males with history of high association <i>After:</i> Biased toward protectors and males with history of high association
Mating: Which males do females mate with in pregnancy?	Those with whom they had low mating rates before conception	Those with whom they had high mating rates before conception
Dyadic Aggression: Within dyads, which males are least aggressive toward females?	Those with the highest mating rates	Sires, relatives, grooming, and association partners
Received Aggression: Which factors reduce rates of received aggression?	Number of partners for grooming, mating, and association decreases aggression received	Strength of grooming, mating and association partners decreases aggression received

3.2 Methods

3.2.1 Determining paternities

Non-invasive fecal sampling at Gombe allows for extraction of genetic material and genotyping at microsatellite loci, which can be used to determine genetic paternity when samples are also available from the offspring's mother and candidate sires. Most infants are not sampled until the age of two, when collecting a fecal sample becomes logistically feasible; therefore, information on paternity is rarely available for infants who die or disappear in the first two years of life. Because genotyping did not begin until the mid-1990s, individuals who died before this time were not sampled, and therefore paternity cannot be determined for any animals born before 1970. Given these restrictions, I identified 72 infants from the Kasekela (KK) and Mitumba (MT) communities whose paternity has been determined by genetic analysis of microsatellite markers (Constable et al., 2001; Wroblewski et al., 2009; Gilby et al., 2013; Feldblum et al., 2014; Walker et al., in press). Although there is no direct paternal care in this species and females mate promiscuously, evidence that females may bias paternity to less related males, as well as concurrent work by Gombe colleagues showing increased interactions between adult males and their own offspring, suggest that paternity may influence male-female interactions across reproductive states (Walker et al., in press; Murray et al., 2016). Therefore, I included sire, a binary variable with reference level "No", as a fixed effect in all models of association, grooming, mating, and aggression, in order to detect any preference for or bias against the sire.

3.2.2 Defining time periods

In order to assess changes in female behavior and sociality across reproductive states, three periods were defined for the mothers of each of the included infants. I used records of swelling to identify conceptive cycles by examining swellings that occurred within the reported range of chimpanzee gestation length, between 208-235 days before birth and for which the day of detumescence could be identified with high certainty (females were observed on days both before and after the recorded detumescence). When records of female estrus met these criteria, I defined the gestation period (“During”) as conception date to infant’s date of birth. When conceptive swellings were not recorded or uncertain, I approximated conception date by counting back from birth, using the community-average gestation length of 225 days (Boehm & Pusey, in prep). I then defined the period of “Before” pregnancy as one year preceding conception, and “After” pregnancy as one year following infant date of birth. Exceptions to these rules occurred when infants died less than one year after birth, in which case the “After” period ended on the date of death. In three cases, the After period of one infant overlapped the Before period for the subsequent infant. I defined the end of the After period and the beginning of the subsequent Before period as the midpoint of the duration of overlap. “Period” as a categorical variable was included as a fixed effect in all models where dyads from more than one period were used, in order to control for the pattern of increased sociality before pregnancy relative to during gestation and after birth (partner preference across periods, grooming preference across periods. The “After” category was set as the reference level in all such analyses.

Here, I present only results from mother-infant pairs in the Kasekela community where infants survived to one year, in order to minimize variation due to differences in community structure and the effects of infant death.

3.2.3 Measures of Dyadic Association

For each of the 216 periods defined above, I calculated the following measures of association and social behaviors between the mother of the infant and each community male using long-term records. All individuals that had reached the age of 12 by the start of the period were included. Twelve is an approximation of the earliest age at breeding observed in both sexes; henceforth, “all males” refers to those included in the analysis based on these criteria. One infant in the dataset was sired by a male younger than 12; this male was included in all periods for the mother of that infant. Dyadic measures of association, grooming, aggression, and mating were z-transformed to account for variation in sociality over time, either across all three periods (BDA) associated with each pregnancy or within each period. I also used raw scores as appropriate for each analysis.

3.2.4 Calculating half-weight index of dyadic association

Party composition data can be queried to find the total number of fifteen-minute scans in a given period during which any two individuals were in the same party, as well as the total number of intervals each individual was observed during that period. I generated these values for each female and all males in the community during the periods defined above. I then calculated the half-weight index of dyadic association (HWI), according to the formula $[Y_{AB}] / ([Y_{AB}] + (0.5([Y_A] + [Y_B] - 2[Y_{AB}])))$, where Y_{AB} is the total number of intervals in which a dyad is observed in the same party, and Y_A and Y_B

are the number of intervals in which individual A and B were observed, respectively (Cairns and Schwager, 1987). While others have calculated this index based on counts of arrivals into a focal party, instead of time spent together, the two measures are highly correlated. I chose to use time spent together to better represent the total time that females spend in parties with males (Foerster et al., 2015). HWI was included as a fixed effect in models of dyadic grooming and aggression rates. Positive effects of dyadic association on grooming would indicate that these measures are concordant and point to concentrated partner preferences; the effect of association strength on received aggression is central to both proposed hypotheses. For each period, I identified each female's highest HWI, and categorized this partner as her top HWI for that period. The strength of this top HWI and the number of non-zero associations were included as factors in the model of total aggression received after pregnancy as a test of whether strong bonds or many partners were more effective in reducing received aggression. HWI before pregnancy was included as a fixed effect in the model of the change in dyadic association strength after conception, to test whether females maintained or diverted investment in established relationships.

3.2.5 Calculating grooming association index

Similar to the dyadic association index, the grooming association index (GAI) is a measure of the time a dyad spends grooming relative to the amount of time they are observed together when one member of the dyad is the focal individual, a restriction imposed because grooming is not consistently recorded for non-focal individuals. From 1978-1997, grooming was recorded in five-minute scans. GAIs in this window are

calculated according to the formula $G_{AB}/(S_A + S_B)$, where G_{AB} is the number of intervals where dyad AB is seen grooming and S_A and S_B are the number of scans where A is focal and B is present, or B is focal and A is present, respectively. Starting in 1998 and continuing to present, grooming bouts have been recorded in and extracted from long-hand notes, yielding durations in minutes. In this window, GAI is calculated according to the same formula, where G_{AB} is the total duration in minutes of grooming between dyad AB and S_A and S_B are the number of minutes each was observed as focal while the other was present. Similar to HWI, GAI was included as a fixed effect in models of dyadic association strength and aggression rates to test whether females tend to associate and groom with the same or different males, and whether these relationships lead to more or less aggression for the female. As with HWI, I designated each female's highest GAI score as her top partner. The strength of her top GAI and the number of non-zero grooming associations were included as factors in the model of total aggression received after pregnancy as a test of whether strong bonds or many partners were more effective in reducing received aggression.

3.2.6 Calculating rates of aggression

Aggressive events were defined as a chase, display, or physical attack directed at the recipient alone; that is, a male displaying at the party is not an instance of dyadic aggression. I calculated rates of dyadic aggression within periods as the number of aggressive events in which the female was the recipient and her male partner was the aggressor, divided by the amount of time the dyad was observed together in that period (Y_{AB}). As a fixed effect in models of association strength, grooming, mating, and

aggression in later periods, this measure tests whether females preferred or avoided more aggressive males as social partners. I also calculated the rate of aggression received by each female in each period from all individuals over 12, from females only, and from males only, by dividing the number of aggressive events in each category by the total time the female was observed in that period (Y_A).

3.2.7 Calculating rates of mating

Copulations are extracted from long-hand notes; mating attempts that were flagged as failures were excluded from this analysis. Because mating occurs almost exclusively while females are fully swollen, I calculated dyadic mating rates as the number of successful copulations divided by the total number of hours the dyad spent together while the female was fully swollen in a given period.

3.2.8 Determining dominance ranks

Dominance ranks were calculated separately among males and females using a modified Elo method. In the classic application of Elo ranking, individuals all receive identical starting positions, and their Elo scores are updated continuously based on each new dominance interaction (Elo, 1978). Franz *et al.* (2015) and Foerster *et al.* (2016) used maximum likelihood modeling to determine individuals' initial scores and the constant k , which is used to calculate the “winner's bonus” and the “loser's tax”, such that these parameters best fit the dataset of observed interactions. Daily Elo scores of all adults can be used to calculate the proportion of same-sex community members dominated by the individuals of interest. I averaged these daily proportion-dominated values within each period for each female and her male associates. Female rank and male

rank were included as fixed effects in all models of dyadic variables due to the established effect of rank on the reproductive strategies and social behaviors of all individuals.

3.2.9 Measures of dyadic relatedness

I used Queller and Goodnight (1989) dyadic relatedness based on microsatellite markers, as calculated by Walker *et al.* (in press). Primates of both sexes tend to bias social behavior towards kin, even paternal kin, with whom they were not reared (Smith *et al.*, 2003; Gilby and Wrangham, 2008; Seyfarth *et al.*, 2013; Tinsley Johnson *et al.*, 2014; Foerster *et al.*, 2015). I included relatedness as a fixed effect in all models of dyadic association, grooming, mating, and aggression, as it is a likely determinant of partner preferences.

3.2.10 Calculating delta HWI

I quantified the change in association within dyads between periods by subtracting the raw HWI before pregnancy from the HWI during pregnancy (delta HWI).

3.2.11 Calculating evenness

To quantify variation in the distribution of females' associations with different males, I calculated the evenness of each female's associations during each period, using a measure commonly used in community ecology to quantify species diversity (Magurran, 1988). I followed Bronikowski and Webb (1996) in extending this measure to alternative uses. Here, evenness is a function of the strength of each dyadic association and the total number of possible associations: $Evenness = -(\sum (p_i \ln(p_i)) / \ln(n))$. In this context, p_i is the

HWI for each association, and n is the number of adult males in the community during that period. In some cases females never associated with particular males, yielding an HWI of zero. Because the natural log of zero is undefined, I added 0.0001 to each HWI in order before calculating evenness. I used each female's evenness score as a fixed effect in the model of delta HWI to examine whether the distribution of relationships before pregnancy affected changes in individual relationships after conception.

3.2.12 Data analysis

To test the hypotheses and predictions outlined in the introduction, I ran a series of linear mixed models (LMM). I performed model selection using corrected Akaike information criteria (AICc) a measure of the fit of the model to the data based on maximum likelihood (Akaike, 2011; Burnham et al., 2011), and present the parameter estimates of all models within two points of the AICc score of the best model ($\Delta < 2$). When multiple best models were found, I performed model averaging to calculate coefficients across all best models, where the contribution of each model is weighted according to its AICc score. I also present AICc weights. All models were performed in R (R Development Core Team, 2014) using the package lme4 (Bates *et al.*, 2014). Model selection, averaging, and AICc weight calculation were performed using the package MuMin (Barton, 2014).

3.3 Results

3.3.1 Partner preference

The protection hypothesis predicts that females will preferentially associate with those males that are most likely to provide protection to them and their offspring after

birth: sires, high-ranking, or closely related males, while the promiscuity hypothesis predicts that male-female associations are not biased according to male characteristics. In the averaged model of association strength across BDA periods (n = 1561 dyads among 21 females and 21 males), females have the strongest associations before conception (coefficient = 0.5007) and the weakest associations (coefficient = -0.4148) during pregnancy. Male rank had a negative effect on association strength (coefficient = -0.2509), such that females associate more with lower-ranking males. Females also associate more with the sires of their offspring (coefficient = 0.1604). Results from all best models are shown in Table 18, and marginal effects of the fixed effects that appeared in at least one of the best models are illustrated in Figure 1.

Table 18: Factors influencing dyadic association strength across periods

Model							
Fixed Effects	1	2	3	4	5	6	Avg
F Rank							
M Rank	-0.2463	-0.2345	-0.2632	-0.2468	-0.2733	-0.2565	-0.2509
Sire				0.1678		0.1509	0.1604
Dyadic Agg Rate							
Relatedness							
GAI	0.067				0.0649	0.0637	0.0657
Mating Rate	0.071				0.0683		0.0697
Before	0.5276	0.5172	0.4399	0.5168	0.4529	0.5267	0.5007
During	-0.4065	-0.4078	-0.4351	-0.4084	-0.4327	-0.407	-0.4148
AICc	4147.12	4147.43	4148.23	4148.39	4148.41	4148.91	
Delta	0	0.31	1.11	1.28	1.29	1.79	
Weight	0.2568	0.2203	0.1475	0.1355	0.1348	0.1051	

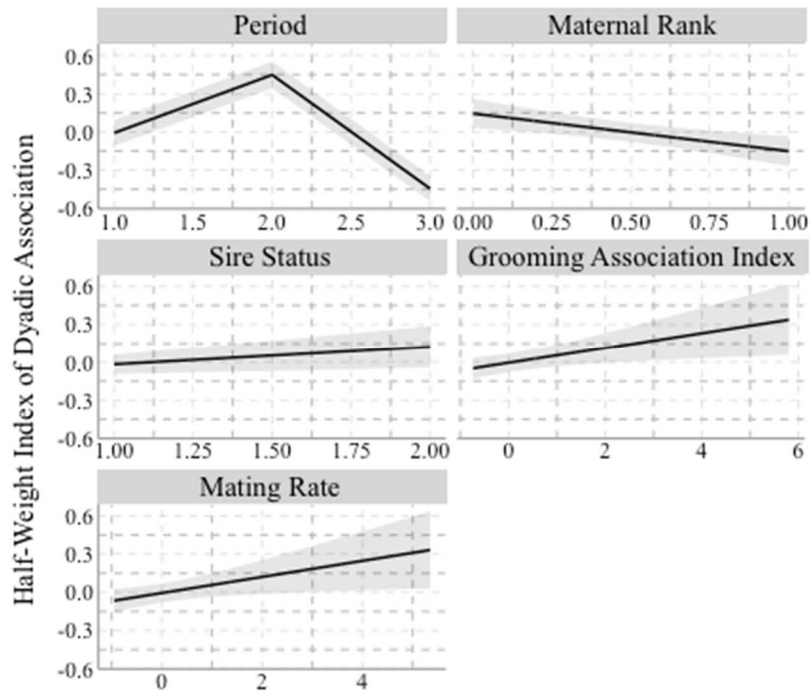


Figure 8: Marginal effects on half-weight index (HWI). Clockwise from top left: Period (after pregnancy = 1, before pregnancy = 2, during pregnancy = 3), maternal rank (average proportion dominated), standardized grooming association index, standardized hourly mating rate, sire (1 = not sire, 2 = sire). Predicted values are drawn from the full model. Shaded areas indicate 95% confidence intervals.

Given the strong effects of period on association strength, I ran separate models for each period type (before, during, and after). Model selection yielded three best models in the Before period (Table 19). Before pregnancy ($n = 522$ dyads among 21 females and 21 males), females associate more with lower-ranking males (average coefficient = -0.2394) and those with whom they have stronger grooming associations (average coefficient = 0.2124) and from whom they receive more aggression (average coefficient = 0.1076).

Table 19: Factors influencing dyadic association strength before pregnancy

Fixed Effects	Model			
	1	2	3	Average
F Rank				
M Rank			-0.2394	-0.2395
Sire				
Dyadic Agg Rate		0.1076		0.1076
R				
GAI	0.219	0.1923	0.2196	0.2124
Mating Rate				
AICc	1425.53	1427.01	1427.3	
Delta	0	1.479	1.771	
Weight	0.5291	0.2526	0.2182	

During pregnancy (n = 522 dyads among 21 females and 21 males; Table 20), female rank is negatively associated with and the only predictor of dyadic association (coefficient = -1.1857); higher ranking females have weaker associations with males during pregnancy.

Table 20: Factors influencing dyadic association strength during pregnancy

Model	Fixed Effects									AICc
	F ID	M ID	F Rank	M Rank	Sire	Dyadic Agg Rate	R	GAI	Mating Rate	
1			-1.1186							1193.74

After giving birth, high-ranking females have stronger associations (average coefficient = 0.6038) than lower-ranking females, while all females continue to associate more with low-ranking males (average coefficient = -0.3905). Dyads with higher levels

of male aggression also have higher association levels (average coefficient = 0.1147), and higher mating rates have a negative effect (average coefficient = -0.3094) on association (n = 522 dyads among 21 females and 21 males; Table 21). However, it should be noted that very few dyads mate in the year after birth.

Table 21: Factors influencing dyadic association strength after pregnancy

Fixed Effects	Model			
	1	2	3	Average
F Rank	0.5616	0.6303	0.6652	0.6038
M Rank	-0.387	-0.4004	-0.3858	-0.3905
Sire				
Dyadic Agg Rate		0.1147		0.1147
R				
GAI				
Mating Rate			-0.3094	-0.3094
AICc	1255.04	1256.21	1256.65	
Delta	0	1.17	1.61	
Weight	0.4991	0.2783	0.2226	

3.3.2 Grooming partner preference

Because association alone may not reflect female partner preferences for males, I ran the same models as above, looking for factors influencing dyadic grooming association, while controlling for association. Predictions for each model were the same as for association. Across periods (n = 1561 dyads among 21 females and 21 males; Table 22), females groom more with the sires of their offspring (coefficient = 0.239) and with more aggressive males (coefficient = 0.1078). This preferential grooming

relationship with sires is not expressed before pregnancy (511 dyads, 21 males, 21 females; Table 23), when females have stronger grooming relationships with those males they spend more time with (coefficient = 0.0981) and again, more aggressive males (coefficient = 0.1586). During pregnancy (n = 522 dyads, 21 males, 21 females; Table 24), females continue to groom with more aggressive males (average coefficient = 0.1442), but also with high-ranking males (average coefficient = 0.3085) and the sires of their offspring (average coefficient = 0.3056). Marginal effects of variables appearing in the best models are illustrated in Figure 9. After pregnancy (n = 528 dyads, 21 males, 21 females; Table 25), females continue to groom more with sires (average coefficient = 0.2847) and high-ranking males (average coefficient = 0.1703), as well as with more closely related males (average coefficient = 0.3461). Dyadic aggression does not appear as a factor in best models after pregnancy.

Table 22: Factors influencing dyadic grooming association strength across periods

Model	Fixed Effects							AICc
	F Rank	M Rank	Sire	Dyadic Agg Rate	R	HWI	Mating Rate	
1			0.23902	0.1078				4328.24

Table 23: Factors influencing dyadic grooming association strength before pregnancy

Model	Fixed Effects									AICc
	F ID	M ID	F Rank	M Rank	Sire	Dyadic Agg Rate	R	HWI	Mating Rate	
1						0.1586		0.09807		1095.32

Table 24: Factors influencing dyadic grooming association strength during pregnancy

	Model				
Fixed Effects	1	2	3	4	Average
F Rank					
M Rank			0.3171	0.2948	0.3085
Sire		0.3131		0.2931	0.3056
Dyadic Agg Rate	0.153	0.1431	0.1408	0.1322	0.1442
Relatedness					
HWI					
Mating Rate					
AICc	1631.82	1632.35	1632.44	1633.37	
Delta	0	0.54	0.63	1.56	
Weight	0.3385	0.2586	0.2474	0.1554	

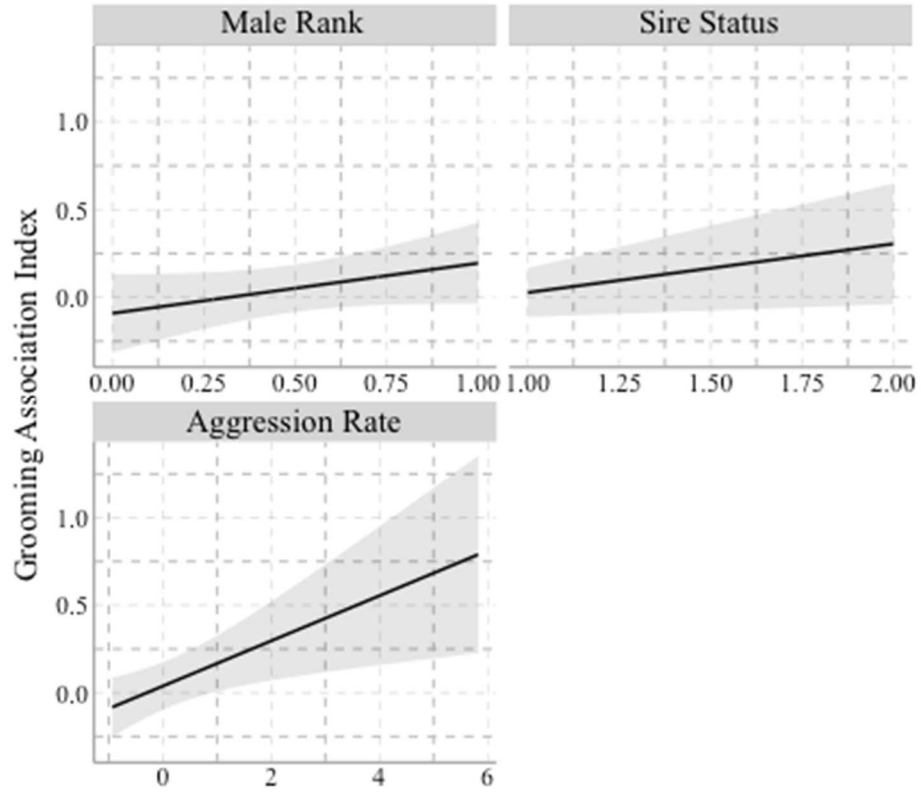


Figure 9: Marginal effects on standardized grooming association strength during pregnancy. Clockwise from top left: Male rank (average proportion dominated), sire (1= not sire, 2 = sire), standardized aggression rate. Predicted values are drawn from the full model. Shaded areas represent 95% confidence intervals.

Table 25: Factors influencing dyadic grooming association strength after pregnancy

Fixed Effects	Model				
	1	2	3	4	Average
F Rank					
M Rank				0.1703	0.1703
Sire	0.2718		0.3009		0.2847
Dyadic Agg Rate					
Relatedness		0.3228	0.3719		0.3461
HWI					
Mating Rate					
AICc	1514.68	1514.93	1515.14	1516.55	
Delta	0	0.25	0.46	1.88	
Weight	0.3652	0.2373	0.2090	0.1885	

3.3.3 Shifts in dyadic association after conception

The promiscuity hypothesis predicts that females should spend time with all available partners in order to confuse paternity. Therefore, females may spend more time in later periods associating with males with whom they previously had weak associations, while decreasing the strength of previously strong associations. Furthermore, I tested the effects of the evenness of each female's associations before pregnancy on the amount of change within dyads after conception (delta HWI); females with evenly distributed associations before pregnancy may be less likely to shift those associations after conception. I also included female and male rank, as well as sire status and relatedness, in the full model (n = 48 pregnancies in 22 females; Table 26). Stronger associations

decreased more after conception than did weaker associations, which were more likely to remain stable or increase (coefficient = -0.9608). Higher-ranking females also experienced greater decreases in their associations after conception (coefficient = -0.2942). However, females with more evenly distributed associations before pregnancy showed more negative change in associations (coefficient = -0.2535).

Table 26: Factors influencing changes in dyadic association after conception

Model	Fixed Effects						AICc
	F Rank	M Rank	HWI Before	Sire	Relatedness	Evenness Before	
1	-0.2942		-0.9608			-0.2535	-558.93

3.3.4 Mating partner preference

Consistent with the promiscuity hypothesis, most females mate with all or nearly all males in the community in the year before conception (average = 83.34%, SD = 22%, mode = 100%, median = 92.31% of males). The promiscuity hypothesis also predicts that females will mate more during pregnancy with males with whom they had lower mating rates before pregnancy, in order to maximize mating across partners, while the protection hypothesis predicts that females will continue to mate at high rates with the same partners across periods in order to strengthen these connections. Therefore, the promiscuity hypothesis predicts a negative association between dyadic mating rate before and during pregnancy, while the protection hypothesis predicts a positive association between mating rates in these periods. I tested the effects of dyadic mating rate before pregnancy on dyadic mating rate during pregnancy, while controlling for both female and male age

and rank, relatedness, and sire status. Model selection yielded a single best model (Table 27); mating rate before pregnancy positively predicted mating rate during pregnancy (coefficient = 0.2241, Figure 10).

Table 27: Factors influencing dyadic mating rate during pregnancy

Model	Fixed Effects							AICc
	Mating Rate Before	F Age	F Rank	M Age	M Rank	R	Sire	
1	0.2241							-1958.61

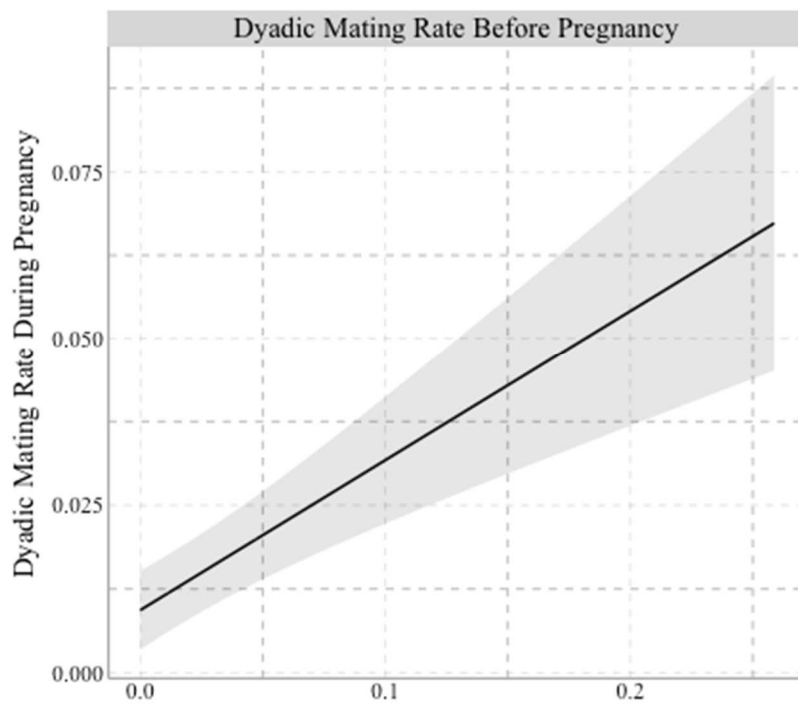


Figure 10: Marginal effect of dyadic mating rate before pregnancy on dyadic mating rate during pregnancy. Predicted values are drawn from the single best model based on AICc. Shaded area indicates 95% confidence interval.

3.3.5 Received Aggression

The protection hypothesis predicts that sires, relatives, and close associates will be less aggressive to females. The promiscuity hypothesis predicts that males will be more aggressive to females with whom they have low mating rates. I tested the effects of association, grooming, and mating, on rates of received aggression within male-female dyads, while also controlling for paternity status, dyadic relatedness, age, and rank of both members of the dyad (1536 dyads, 22 males, 21 females). I used unstandardized rates for mating and grooming to reflect the real variation present in the sample. Model selection yielded one best model (Table 28), in which male and female rank both positively predict aggression within a dyad (male rank coefficient = 0.0039, female rank coefficient = 0.0052); high-ranking females receive more aggression from their male partners, and high-ranking males are more aggressive toward their female partners.

Table 28: Factors influencing rates of dyadic aggression within periods

Model	Fixed Effects									AICc
	F Rank	M Rank	Period (Before)	Period (During)	R	Sire	HWI	GAI	Mating Rate	
1	0.0052	0.0039								-10133.07

I then tested whether relationships in earlier periods affected aggression received by females from their male partners after birth (Table 29). Lactating females received less aggression from those males with whom they had groomed before pregnancy and mated during pregnancy (average GAI coefficient = -0.0374; average mating coefficient = -0.0115).

Table 29: Factors influencing rates of dyadic aggression after pregnancy

Fixed Effects	Model		
	1	2	Average
F ID			
M ID			
F Rank			
M Rank			
Sire			
HWI Before			
HWI During			
Mating Before			
Mating During		-0.0115	-0.0115
GAI Before	-0.0374		-0.0374
GAI During			
Agg Before			
Agg During			
AICc	-3804.9	-3803.32	
Delta	0	1.58	
Weight	0.6876	0.3124	

Looking beyond dyadic rates of aggression, I examined the overall rate of aggression received by each female after pregnancy (n = 48 pregnancies in 22 females). The promiscuity hypothesis predicts that having more partners for association, grooming, and mating, rather than the strength of associations, will lead to reduced aggression. The protection hypothesis predicts the opposite, that strong associations result in less received aggression for females. Therefore, I tested the effects of mating rates before and during pregnancy, the number of mating partners, the number of grooming and association partners, the absolute strength of the female's strongest association in each of these measures, and the evenness of associations before and during pregnancy, on the overall rate of aggression received by each female after pregnancy. I first examined aggression

received from all individuals over 12: model selection yielded a single best model in which the only predictor variable was the strength of the top GAI partner before pregnancy (coefficient = -0.549). Females with a strong grooming association before pregnancy received less aggression after pregnancy. I then ran the same full model with aggression received from males as the outcome variable; model selection again resulted in a single best model with the same single predictor variable. Similarly, females with the strongest top GAI before pregnancy received less aggression from males (coefficient = -0.3356, Figure 11). These results are summarized in Table 30. Finally, I tested the effects of the same factors on aggression received from females after pregnancy. Females with strong grooming partners before and during pregnancy, and higher mating rates during pregnancy, received less aggression from other females after pregnancy (Table 31).

Table 30: Factors influencing rate of aggression received after pregnancy

Fixed Effect	All received aggression	Aggression received from males
F Rank		
Mating rate before		
Mating rate during		
Mating partners Before		
Mating Partners During		
Top GAI before	-0.0549	-0.3356
Top GAI during		
Grooming partners before		
Grooming partners during		
Top HWI before		
Top HWI during		
Association partners before		
Association partners during		
Evenness before		
Evenness during		
AICc	-410.3002	-250.5189

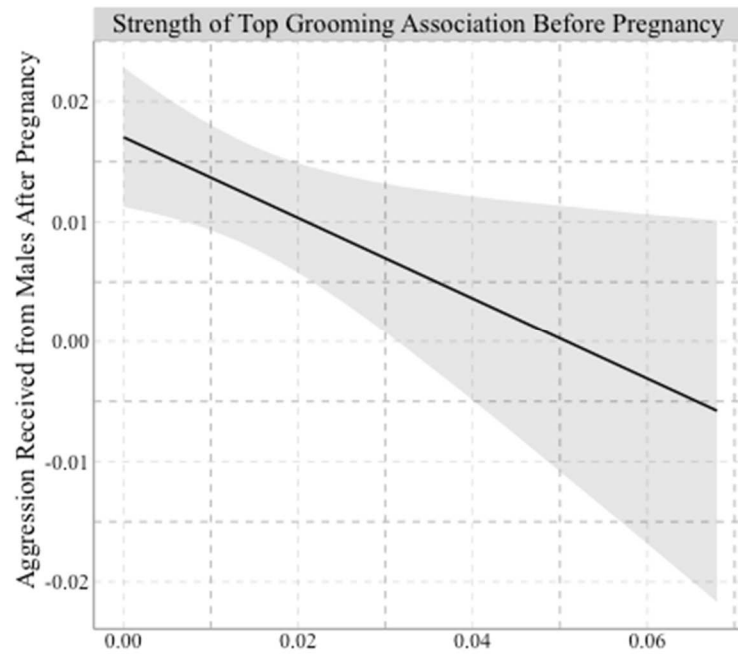


Figure 11: Effect of the strength of the top grooming association before pregnancy on received aggression from males after birth (hourly rate). Predicted values are drawn from the single best model based on AICc. Shaded area indicates 95% confidence interval.

Table 31: Factors influencing rate of aggression received from females after pregnancy

Fixed Effect	Model			
	1	2	3	Average
F Rank				
Mating rate before				
Mating rate during			-0.0216	-0.0216
Mating partners Before				
Mating Partners During				
Top GAI before	-0.0245			-0.0245
Top GAI during		-0.014		-0.014
Grooming partners before				
Grooming partners during				
Top HWI before				
Top HWI during				
Association partners before				
Association partners during				
Evenness before				
Evenness during				
AICc	-452.99	-452.54	-452.15	
Delta	0	0.4519	0.8461	
Weight	0.4077	0.3252	0.2671	

3.4 Discussion

3.4.1 Broad patterns in sociality

Females' associations with males are highest in the year before pregnancy, drop to their lowest levels during gestation, and rebound slightly after the birth of their infant. Given that most females will copulate with all or nearly all adult males in the community before conceiving, it is not surprising that they spend so much time with males during

this cycling phase, and the elevated gregariousness of cycling females is well documented in chimpanzees (Goodall, 1986; Matsumoto-Oda, 1999a; Williams et al., 2002; Otali and Gilchrist, 2006; Wakefield, 2013). This pattern is visible in all females, but high-ranking females show a greater decrease in sociality during pregnancy and higher levels of association after pregnancy, relative to lower-ranking individuals. Low-ranking lactating females exhibit higher levels of fecal glucocorticoid concentrations, suggesting greater stress, when participating in large parties (Markham et al., 2013), which may prevent them from associating with males.

Male-female bonds are also sensitive to female reproductive state and rank in other species, especially those characterized by intersexual “friendships.” Friendships are well documented in baboons and macaques and are thought to improve infant survival as a means of defense against infanticide (Palombit, 2000, 2009; Baniel et al., 2016). In wild chacma baboons, for example, higher-ranking females had stronger friendships with males after giving birth, and friendships were weakest during pregnancy. This is consistent with an infanticide-avoidance strategy, since infanticide is impossible during pregnancy, and emphasizes the importance of investing in protective, preferential intersexual bonds (Baniel et al., 2016).

Although male-female associations in chimpanzees are not as obvious or consistent as those documented in cercopithecines, this study supports the conclusion that strong bonds are more effective than many weak bonds at reducing the aggression that females received from males, as predicted by the protection hypothesis.

3.4.2 Evaluating the promiscuity hypothesis

Patterns of association, grooming, and aggression lead me to conclude that females do not associate indiscriminately with males across reproductive states. I instead find only scattered support for the promiscuity hypothesis as an explanation for female social behavior, in spite of the promiscuous mating observed before pregnancy. If females are following a promiscuous strategy to maximize association with a wide number of males, they may avoid investing heavily in the same relationships over time at the expense of others. As predicted by the promiscuity hypothesis, dyads with high association scores before pregnancy show greater decline after conception than dyads with weak associations, while dyads that associated weakly before pregnancy were more likely to stay the same or increase during pregnancy. Association in dyads involving high-ranking females also declined more steeply during pregnancy. However, these results may simply reflect the overall decline in sociality during pregnancy, which is more dramatic in pairs that had previously spent a greater amount of time together. In direct opposition to the prediction that females will mate more during pregnancy with those males which have not been frequent mating partners, within dyads, mating rate before pregnancy positively predicted mating rate during pregnancy. Females continued to mate with the same males during gestation instead of confusing paternity by mating with less frequent partners.

Females with higher overall mating rates during pregnancy received less aggression from females after pregnancy. Although we have not directly tested whether this is a result of male policing of intrasexual aggression, males are known to intervene

on behalf of sexually attractive females (Kahlenberg et al., 2008b). However, in the year after birth, females are typically not sexually receptive, making it less likely that males would act as protectors. The *number* of mating partners did not appear in any of the best models as a predictor of received aggression from males, females, or both. Therefore, we cannot conclude that mating with many partners is more effective in reducing aggression than maintaining a high mating rate with one or a few males. On average, females receive approximately 10 times as much aggression from males as from females in the year after giving birth. Avoiding intrasexual aggression may not be a significant component of female strategy; in Gombe, however, females have been responsible for the majority of infanticides, so the risk of intrasexual aggression is not negligible.

Finally, in the year after birth, dyadic mating rate was negatively associated with association, suggesting that females are not investing in association with their mating partners. Mating rates were generally very low in this period, the presence of a young infant is likely a strong signal of infertility, and given the average interbirth interval of approximately one and a half years (Wallis, 1997; Jones, 2011), it is unlikely that paternity confusion through promiscuous mating during early lactation could contribute to reproductive success. Given that only a handful of dyads were observed to mate in the year after birth, it is unlikely that mating is an important driver of male-female association in this period.

3.4.3 Evaluating the protection hypothesis

Females gain benefits from building strong social relationships with males and maintaining these bonds over time, as predicted by the protection hypothesis. Grooming

bonds emerged as the most meaningful measure of these relationships. I found a positive correlation between grooming and time spent together, looking across all reproductive states, as well as within the year before pregnancy. This is not surprising, given that socio-spatial proximity has been shown to predict high association scores and grooming in other populations (Langergraber et al., 2013; Machanda et al., 2013). Increased mating rate was also correlated with increased association across reproductive states, indicating consistent relations over time.

The protection hypothesis predicts that females will choose to associate closely with males that are most likely and best able to offer protection, including high-ranking males, closely related males, and the sires of their offspring. I found support for all three of these predictions. Looking at dyadic scores across all periods, I found that females spent more time with the sires of their offspring than with other males. However, paternity was not a factor in the best models of dyadic association any single period. This result is concordant with findings from other populations and the traditional view that paternity is obscured and males provide no care to their offspring: Male western chimpanzees did not show any change in association with females after the births of new infants, regardless of sire status, suggesting that association alone may not reflect indirect paternal care or paternity likelihood in chimpanzees (Lehmann et al., 2006). However, grooming rates reveal an intriguing pattern of association between females and the sires of their offspring. Females have higher grooming association scores with sires across periods, as well as during gestation and in the year after birth. This pattern is not apparent in the year before conception, suggesting that females are not simply conceiving with

their closest associates. Although there is no obvious paternal care in chimpanzees, and promiscuous mating should make it difficult for both males and females to detect paternity based on mating history, evidence is accruing in support of paternity recognition and preferential association between offspring and sires. The use of focal data may allow us to detect partner preferences that are obscured in group composition data; in this study, the use of focal data would lead to the exclusion of several hard to follow females. However, Murray et al. (2016) used focal data on males from Gombe to show that they associated more with their own offspring than with unrelated infants in the first 18 months after birth; the effect was strongest in the first six months. In their study, males also interacted (played, groomed) more than expected with their own infants. Elevated rates of play between males and their genetic offspring has also been demonstrated in Tai National Park, Côte d'Ivoire (Lehmann et al., 2006). A similar pattern of father-offspring association has been reported in Assamese macaques, where males associate more closely with mother-infant pairs in the infant's first year of life when they were the sire of the offspring and had been frequent mating partners of the mother (Ostner et al., 2013). These bonds are surprising in a promiscuous mating system, given that even in mountain gorillas, where paternity certainty is high, male-offspring bonds decline as the number of adult males in the community increases, presumably decreasing paternity certainty (Rosenbaum et al., 2016). Lehmann *et al.*, (2006) also found that male chimpanzees directed less aggression to the mothers of their offspring relative to other females in the first 6-12 months of the offspring's life. While this effect is partially explained by the fact that males are less aggressive toward all young infants, aggression rates remained

depressed for the mothers of their own offspring, but not other females, as the infants aged (Lehmann et al., 2006).

Females also showed a preference for grooming with more closely related males, as measured by Queller and Goodnight's R , in the year after they gave birth. This finding aligns with results from Murray and colleagues showing mothers' strong preference for male maternal kin in the months and years after parturition (Murray, pers. comm.). Inclusive fitness theory predicts that related males will be less likely to commit infanticide than unrelated males, making them safe partners in the presence of a vulnerable infant (Hamilton, 1964). Some of the related males identified as preferred partners in this study may be known from experience (e.g. mother's adult sons and maternal brothers) while others may be related through the paternal lineage and therefore not behaviorally identifiable, indicating another mechanism at play for kin recognition. Although this mechanism has not been identified, females in a variety of species show preference for paternal kin (Schülke et al., 2013), while female chimpanzees tend to reproduce with males to whom they are less related than they are to community males on average (Walker et al., in press). The tendency of females to associate, but not reproduce, with male kin highlights the importance of kin recognition for females as they face the dual challenges of avoiding both inbreeding and infanticide.

Finally, both during and after pregnancy, females groomed more with higher-ranking males, whose superior fighting ability likely makes them better protectors. Anestrous females are more likely to initiate grooming bouts with adult males, whereas adult males are more likely to initiate grooming bouts with estrous females (Wallis, 1992;

Slater et al., 2008), suggesting that the pregnant and lactating females in my sample may be responsible for establishing these grooming associations. Females may use grooming to maintain proximity to preferred males; in estrous females, mating frequency, grooming frequency, and male rank are all positively correlated (Matsumoto-Oda, 1999b). However, in Kanyawara, male dominance rank had no effect on grooming rates in male-female dyads (Machanda et al., 2013). Sexual coercion and aggression within dyads may also result in higher grooming rates, as discussed below.

The protection hypothesis predicts that strong bonds with males are associated with reduced rates of aggression received by females after they give birth. The predictor variables that emerged in model selection all support this hypothesis. Looking at all received aggression after birth, I found that females with a strong grooming partner (strength of her top grooming association) before pregnancy received less aggression overall. Restricting the analysis to only aggression received from males, the strength of the top grooming association before pregnancy was the sole factor in the best model. Similarly, those females with stronger grooming bonds both before and during pregnancy received less aggression from other females after pregnancy.

Analysis of aggression in the year after birth within male-female dyads revealed that females received less aggression from those males with whom they had groomed before conceiving, underlining again the importance of grooming bonds in establishing protective relationships. Males with whom they had mated more during pregnancy were also less aggressive toward them; this may offer an explanation for continued sexual swellings and mating during gestation. In Hanuman langurs, both genetic sires and males

who were residents during the conceptive cycle of an infant were observed to intervene in infanticidal attacks. However, males that had copulated with females only post-conception never defended these infants, and in fact were also observed to attack them, suggesting that mating during pregnancy is not an effective defense against infanticide in this species (Borries et al., 1999).

Some results in this study do not align with the predictions of the protection hypothesis. Most striking among these is the finding that females tend to associate more with males that are more aggressive toward them, both across periods and within the year after birth. While females have higher dyadic association indices with low-ranking males, they have stronger grooming relationships with high-ranking males; higher-ranking males are also more aggressive within dyads. These findings challenge the protection hypothesis, since it appears that preferred male partners may themselves be a threat to females. It is possible that females actively pursue association with high-ranking males for protection from intrasexual or intergroup aggression, but expose themselves to aggression from males within their own communities. Meanwhile, low-ranking males join parties with females, increasing their DAI scores with adult females: By monitoring fluctuations in party composition over two days, Matsumoto-Oda (1999a) showed that “sexual parties,” or those containing estrous females, almost always included the alpha male, while the addition of an estrous female to a party led to an increase in the number of lower-ranking and adolescent males. These low-ranking males may be utilizing a “friends with benefits” strategy to increase mating success by maintaining proximity to a particular female, even if they are unable to completely monopolize mating with her

(Ostner et al., 2013). Females' association with aggressive males may also be driven by males, whose reproductive success is improved by long-term, aggressive sexual coercion (Feldblum et al., 2014). Grooming could also be the direct result of increased dyadic aggression, serving as a form of appeasement or reconciliation toward the aggressor (McFarland and Majolo, 2011). Kaburu and colleagues (2015) also found that high grooming rates among eastern chimpanzees did not predict reduced aggression in male-female dyads, and concluded that females were not using grooming as a means to receive protection from males. Instead, victims of aggression may be coerced by their aggressors into giving grooming as a way of repairing the valuable social relationship, alleviating stress, and avoiding further aggression, as in Barbary macaques (McFarland and Majolo, 2011).

It is not clear from these analyses whether males or females are driving both grooming associations and time spent together, but future work will use direction of grooming to probe the role of each member of the dyad in maintaining the relationship. In one study of western chimpanzees, females copulated more frequently with the ultimate sire of her offspring relative to other community males, but sires did not copulate more with mothers of their offspring relative to other females, suggesting that females, but not males, could use copulation rates to recognize paternity (Lehmann et al., 2006). However, given the demonstrable ability of males to identify conceptive cycles and fertile days within cycles (Deschner et al., 2004; Alberts and Fitzpatrick, 2012), it is possible that they glean information on paternity likelihood from the timing of mating with a given female, rather than the frequency. Males may benefit from increased

association with particular females by securing future matings through affiliative behaviors, opportunistic mating, or improved information about her fertility (Langergraber et al., 2013). However, Murray et al. (2016) found that in Gombe chimpanzees, males were not more likely to sire the subsequent offspring of females with whom they had previously reproduced and/or associated closely. Similarly, Baniel *et al.* (2016) found that male-female friendships in baboons weakened after females resumed cycling and were not predictive of future paternities for males. Therefore, these male-female bonds may be more indicative of paternal than mating effort. To further test the protection hypothesis as presented here, additional studies are needed to look specifically at policing behavior and determine whether strong male partners protect lactating females from aggression. Together, the results from this study suggest that females living in a highly promiscuous social system are nonetheless able to gain social benefits by investing in strong relationships with males. This study also adds support to the intriguing idea that paternity may be discernible even when it has been confused by promiscuous mating.

4. Hormone Production during Pregnancy: Correlates of Post-Conception Swellings, Maternal Effects, and Comparison with Preconception Swellings

4.1 Introduction

The relationship between hormones and sexual behavior is apparent across the order Primates, from the short, strictly seasonal estrus characteristic of the Strepsirrhines, to the inventive use of sexual swellings for social bonding in bonobos (reviewed in Dixson, 2012). Advances in laboratory science now permit field researchers to extract steroid hormones, or their metabolites, from urine and feces, allowing for quantitative measures of the endocrinological underpinnings of sexual and sociosexual behaviors and signals. These new methodologies have elucidated the relationship of sexual swellings to critical reproductive events such as ovulation and conception, and, therefore, their reliability as signals of female fertility. Here, I discuss the pattern of hormone production in a typical anthropoid ovarian cycle, including the timing of swelling in relation to ovulation and conception. I then examine the correlation of hormonal changes to sexual swellings, female proceptivity, and male mating interest, as measures of the reliability of the signal. Finally, I discuss the hormonal profiles of pregnancy in several primate species, including chimpanzees, and present new data characterizing the hormonal profile of post-conceptive swellings in chimpanzees.

4.1.1 The typical anthropoid ovarian cycle

While the details and timing vary among species, the “central dogma” of sexual swellings is that rising estrogen during the follicular phase triggers the tumescence of the swelling, whose specialized tissues are densely populated with estrogen receptors

(Dixon, 1983). Ovulation is expected to occur during the period of maximal swelling and is heralded by a brief peak in luteinizing hormone; the few days immediately before and after ovulation are deemed the periovulatory period. Progesterone, rising through the luteal phase following ovulation, inhibits the swelling and leads to detumescence. In species that lack sexual swellings, other estrus behaviors may respond similarly to estrogen and progesterone, increasing in frequency during the follicular phase, peaking during the periovulatory period, and declining in response to progesterone during the luteal phase. Conceptive cycles can often be distinguished from non-conceptive cycles by the persistence of progesterone above baseline levels; in most species, progesterone remains high after conception and increases throughout gestation.

This pattern has been verified through steroid hormone analysis in a number of primates: In crested macaques (*Macaca nigra*), for example, ovarian cycles were reflected in fecal metabolites of estrogen and progesterone; estrogen peaked approximately three days prior to the post-ovulatory rise in progesterone (Higham et al., 2012). In a study of yellow baboons (*Papio cynocephalus*), researchers were able to capture the peak and fall of progesterone across the luteal phase and a peak in estradiol (E_2) at or slightly following detumescence of the sexual skin; however, the E_2 peak was less clear than that in progesterone and was sometimes accompanied by other apparent peaks throughout the cycle (Wasser et al., 1991). Fecal progesterone (P_4) peaked nine days after the onset of maximal tumescence, and had returned to baseline levels 16 days later, framing the luteal phase of the cycle. Fecal E_2 rose for the 10 days of the follicular phase before peaking on the day of maximum tumescence; levels fell steeply in the luteal

phase (Stavisky et al., 1995). A 30-day cycle was detected via fecal E₂ and P₄ in sooty mangabeys (*Cercocebus torquatus atys*), with E₂ twice as high in the follicular phase as in the luteal phase (Whitten and Russell, 1996). In bonobos (*Pan paniscus*), fecal and urine samples were used to measure estrone conjugates (E₁C) and pregnanediol glucuronide (PdG) during the follicular and luteal phases. E₁C increased to five to seven times the baseline level during the follicular phase leading to ovulation, while PdG peaked zero to four days after E₁C. Analysis of these hormones revealed a follicular phase that was highly variable in length (17-40 days) but a much more consistent luteal phase of 11-15 days (Heistermann et al., 1996).

Chimpanzees share the typical primate pattern of estrogen rising through the follicular phase, followed by a progesterone increase in the luteal phase, with ovulation occurring between the two peaks (Graham, 1981). Among Gombe chimpanzees (*Pan troglodytes schweinfurthii*), the average cycle length is 33.8 days in parous females and 39.8 in nulliparous females; maximal swelling lasts for 12-13 days (Wallis, 1997). These values vary slightly among populations but are fairly consistent (Matsumoto-Oda, 1999a; Emery and Whitten, 2003). Within the nearly two-week period of maximal tumescence, several studies have found that conception is most likely to result from matings that occur between four to seven days before detumescence, given the lifespan of sperm and the likely timing of ovulation at or near the day of detumescence (Dixson, 1983; Dahl et al., 1991; Wallis, 1997; Deschner et al., 2003; Emery and Whitten, 2003; Emery Thompson, 2005; Deschner and Boesch, 2007).

4.1.2 Reliability of sexual swellings as signals of fertility

In spite of the strong relationships between hormonal cues and sexual swellings across the ovarian cycle, information provided by sexual swellings may be imperfect at best in many species. In sooty mangabeys, for example, the E₂ peak in preconception cycles was found to be highly variable in relation to maximal swelling, suggesting that the swelling is not a precise signal of ovulation in this species, even during fertile periods (Whitten and Russell, 1996). Another hypothesis is that the size of sexual swellings offers a reliable signal of female quality, relating swelling size to measures of lifetime reproductive success in olive baboons (*P. anubis*) (Domb and Pagel, 2001). However, these inter-individual differences may be better explained by body size (Zinner et al., 2002). In yellow baboons, sexual swelling size increased in successive cycles from resumption of cycling following post-partum amenorrhea to conception, suggesting that within-female changes from cycle to cycle offer a reliable signal of the probability of conception (Fitzpatrick et al., 2014). The number of cycles since amenorrhea was the strongest predictor of male consortship choice; absolute swelling size was not (Fitzpatrick et al., 2015). This study also found no relationship between swelling size and measures of lifetime fitness.

Substantial work in the genus *Macaca*, in which sexual swellings are common but not ubiquitous, has explored the relationship between hormones, swellings, and female sexual behavior. In wild Assamese macaques (*M. assamensis*), no consistent relationship could be found between E₁C and the size of subcaudal sexual swellings. Some females exhibited peak swelling before conception, others after, and some showed no swelling at

any point in the cycle (Fürtbauer et al., 2010). These authors concluded that sexual swellings in Assamese macaques do not convey information about female reproductive condition, and may instead be a relic of an ancestral trait (Fürtbauer et al., 2010). Sexual swelling size, but not female-initiated copulatory behavior, correlated strongly with the rise of estrogen levels approaching the day of the ovulation in Barbary macaques (*M. sylvanus*). Males exhibit more ejaculatory copulatory behavior during the most fertile phase of females' ovarian cycles. Ejaculations are correlated with the size of the sexual swelling both leading to and following ovulation, as determined by the peak in fecal progesterone (Brauch et al., 2007). This suggests that sexual swelling size is an honest signal of female fertility, while behavioral clues, which do not vary significantly across the cycle, are not. However, in crested macaques (*M. nigra*), both sexual swelling size and some female behaviors, such as solicitation, presents, look-back, and lip-smacks: all signals of female proceptivity were associated with the ratio of estrogen to progesterone (E:P). Males were responsive to these cues, mounting and mating more when females were closer to ovulation. These behaviors were also elevated during conceptive cycles relative to non-conceptive cycles, indicating that males are sensitive to both within- and between-cycle variation in fertility (Higham et al., 2012). Male hamadryas baboons (*P. hamadryas*) consorted more with females who were maximally swollen although female proceptive behavior did not change predictably during maximal swelling (Higham et al., 2009).

Female Japanese macaques (*M. fuscata*) do not display sexual swellings, but female proceptivity and reddening of the face during the follicular phase may provide

some information about female fertility to males (Rigaill et al., 2015). In this species, these signals also honestly signal female reproductive state: After conception, females' faces become darker and less red, and proceptive behaviors such as approaching and grooming males are significantly less frequent (Rigaill et al., 2015). No copulations occurred during pregnancy, suggesting that these cues were adequate to alter male behavior and minimize non-conceptive mating. Similarly, in both chacma (*P. ursinus*) and yellow baboons, changes in the color of the sexual skins indicate pregnancy, offering a clear cue of infertility to males (Altmann, 1973).

As described in the introductory chapter, post-conception swellings occur in a variety of species, further muddying the water of the information content of the swelling. Sooty mangabeys also exhibit a single, stereotyped perineal swelling approximately 49 days following conception (Gordon et al., 1991). As in preconception cycles, post-conception swellings were associated with a high ratio of estrogen to progesterone, and females mated multiply during them. However, further work showed that while subordinate males mated, alpha males did not mate with pregnant estrous females, and may have used differences in the patterns of estrogen and progesterone peaks to discriminate between fertile and infertile cycles (Gordon et al., 1991; Gust, 1994). These results highlight the importance of understanding the temporal relationship between sexual swellings and reproductive events before drawing conclusions about their function as a signal, honest or deceptive, of female fertility.

Evidence from hormonal and behavioral data in chimpanzees supports the view that swelling size offers a reliable signal of fertility and female condition during that

cycle (Emery and Whitten, 2003). In captive chimpanzees, sexual swelling size is positively and significantly correlated with E₂ in the early follicular and early luteal phases, and with the length of elevated progesterone during the luteal phase (Emery and Whitten, 2003). Female proceptive behavior is highest during maximal tumescence. Behavioral studies confirm that males are sensitive to these shifts and adjust their behavior accordingly. Nishida (1997) found that males inspect the genitals of cycling females eight times more often than lactating or pregnant females; these inspections peak several days before the onset of maximal tumescence. Females in Kanyawara copulated at significantly higher rates during the periovulatory period, as determined by peak estrogen concentrations, and during the periovulatory periods of conceptive cycles as compared to the same window during non-conceptive cycles (Emery Thompson, 2005; Emery Thompson and Wrangham, 2008). Alpha males were more likely to copulate during the periovulatory period while younger and lower ranking males mate more early in tumescence (Deschner et al., 2004; Emery Thompson, 2005; Nishida, 1997). Studies of captive chimpanzees found that females receive more grooming from their male cage-mates during the follicular phase, but groom these males more during the luteal phase of their cycle. (Wallis, 1992). In Mahale National Park, Tanzania, grooming and copulation rates were correlated, with highest frequency of both during the last three days of full swelling before detumescence (Matsumoto-Oda, 1999a). In spite of the demonstrated sensitivity of male chimps to female cues of fertility, mating during post-conception swellings does occur in both captive (Wallis and Lemmon, 1986) and wild settings (Wallis and Goodall, 1993). In fact, males initiated more copulations with pregnant,

swollen females than with non-pregnant, swollen females, and pregnant females were more receptive to copulation attempts, leading to higher rates of successful copulation during pregnancy (Wallis, 1982).

4.1.3 Hormone production during gestation in primates

Together, results from fecal and urine sampling across primates have helped to clarify patterns of steroid hormone production at conception and during gestation. Pregnancy is detectable via hormone assay throughout gestation in a number of primate species where it has been tested: during the last two months of pregnancy, primiparous yellow baboons show significantly higher levels of fecal estrogen metabolites relative to multiparous females (Altmann et al., 2004).

Fecal samples from wild Assamese macaques were analyzed via enzyme immunoassay (EIA) for concentrations of E_1C and 20α -dihydroprogesterone (20α -OHP). While 20α -OHP rose steadily through gestation, E_1C showed only a slight increase before dropping (Fürtbauer et al., 2010). In wild Barbary macaques, fecal hormones were used to identify the periovulatory period, defined by the rise of progesterone two standard deviations above the mean of the previous five samples. Pregnancy was determined to occur when these elevated progesterone levels persisted for at least two samples after the time of ovulation; in one representative female, estrogen also remained high following conception (Möhle et al., 2005). Similarly, pregnancy was detectable in fecal P_4 measures in captive pigtailed macaques, which remained elevated after the luteal phase and continued to rise throughout gestation (Wasser et al., 1988). Fecal PdG alone was sufficient to detect cycles and conception in Hanuman langurs

(*Presbytis entellus*). Interestingly, in spite of luteal-levels of PdG for the first half of pregnancy, and further increases in the second half, females of this species do exhibit post-conception estrus that typically occurs approximately halfway through their 211-day gestation (Ziegler et al., 2000). In one study of bonobos, in both fecal and urine samples, all estrogen and progesterone assays were significantly elevated in pregnant relative to non-pregnant females, and all increased throughout pregnancy; the rise in fecal steroids was not as pronounced as that seen in urinary steroids. Of all the estrogens, estriol (E₃) showed the greatest increases during the late stages of gestation (Heistermann et al., 1996). Urine samples from captive pregnant chimpanzees confirmed that both E₁C and PdG rise throughout gestation (Shimizu et al., 2003).

The studies presented above illustrate that noninvasive sampling of fecal or urinary hormone metabolites has proven instrumental in the study of reproductive parameters of both wild and captive primates. Validation of these techniques is crucial, and can be established through comparison with serum hormone levels in captive populations, darting of wild animals (Faiman et al., 1981; Wasser et al., 1988; Whitten and Russell, 1996), or through a biological validation; for example, testing to confirm that assays of progesterone are significantly and consistently higher during pregnancy than in postpartum amenorrhea (Altmann et al., 2004).

4.1.4 Aims

As described in the introductory chapter, post-conception swellings occur in a variety of species, presenting a mechanistic puzzle. Here, I use urinary steroid hormones to build a hormonal profile of swellings during pregnancy in chimpanzees, with four

specific aims. First, I ask how estrogen and progesterone levels change over gestation. Based on earlier reports, I expect that both hormones will increase significantly as pregnancy progresses (Faiman et al., 1981; Shimizu et al., 2003). Second, I ask how estrogen and progesterone change during post-conception swellings with the prediction that, as in preconception cycles, elevated estrogen and decreased progesterone will be associated with swellings. Third, I compare concentrations of estrogen and progesterone during post-conception swellings to published reports of these hormones during preconception swellings. I expect that both hormones will be elevated relative to their respective preconceptive peaks. Finally, I ask whether the observed tendency for younger females to swell more than older females during pregnancy has a hormonal underpinning, with the prediction that younger females exhibit higher concentration of E₂ during pregnancy.

4.2 Methods

4.2.1 Urine sample collection

Urine samples were collected by M. Emery Thompson from known female chimpanzees in the Kasekela community at Gombe National Park, Tanzania, and in the Kanyawara community in Kibale National Park, Uganda as part of her study of the hormonal correlates of sexual swellings, mating, and conceptions (Emery Thompson, 2005). Samples were only collected when no contamination with feces occurred, and only when urination was directly observed, to ensure the identity of the individual. Urine was pipetted from leaves or plastic sheeting held under an individual resting arboreally. While most samples were collected before noon, some were collected as late as 7:30 pm.

However, Emery Thompson (2005) found no significant effect of the time of sample collection in samples from cycling non-pregnant females collected during the period and from the same communities on concentrations of E₂ or progesterone, indicating that there is no circadian pattern in excretion of these reproductive hormones in urine. Samples were stored on ice until they could be frozen, and were kept frozen until the time of assay.

4.2.2 Assays

Laboratory assays were conducted by M. Emery Thompson in the Primate Reproductive Ecology Laboratory, Department of Anthropology, Harvard University. Competitive enzyme-immunoassay (EIA), an assay that relies on competitive binding of steroid hormones to an antibody, was used to measure E₁C and PdG (Czekala et al., 1986; Shideler et al., 1990). Samples were corrected for the creatinine levels to control for the water content of the urine (Tausky, 1954). Only samples with creatinine concentrations above 0.08 were included in the analysis.

4.2.3 Determining estrous state and pregnancy

When females were observed and sampled around the time of conception, the start of pregnancy was determined by identifying sustained elevations of E₁C and PdG. Otherwise, conception date was assigned by counting back 230 days from offspring birth. Pregnancy was confirmed by post-hoc testing of urine samples with commercially available human pregnancy tests, which detect the presence of chorionic gonadotropin.

Sexual swellings were evaluated visually and assigned a rating of 1-3, where 1 is complete detumescence, 2 is partial tumescence, and 3 is full tumescence. These ratings

correspond to the fractional rating scale used in Gombe records, with scores of 0.25-0.75 all classified as a score of 2.

4.2.4 Data analysis

Creatinine-corrected E₁C and PdG concentrations were averaged among same-day samples. E₁C is expressed as pg/ml urine; PdG as µg/ml urine. These values were log-transformed before statistical analyses. I addressed the first and last aims together, by modeling the effects of trimester and maternal age on E₁C and PdG, while controlling for swelling state, using linear mixed models (LMM) with log-transformed E₁C and PdG as outcome variables. To address the second aim, determining changes in estrogen and progesterone during post-conception swellings, I performed generalized linear mixed models (GLMM) with a binary outcome variable of estrous state (0 = no swelling, 1 = partial or full swelling) with log E₁C and PdG as fixed effects, controlling for trimester and pregnancy id as a random effect. All models were performed in R (R Development Core Team, 2014) using the package lme4 (Bates *et al.*, 2014). I performed model selection using corrected Akaike information criteria (AICc) a measure of the fit of the model to the data based on maximum likelihood (Akaike, 2011), and present the results of all models within two points of the AICc score of the best model (delta <2). I also present AICc weights. When multiple best models were found, I performed model averaging to calculate effect sizes across all best models, where the contribution of each model is weighted according to its corrected AICc score, which corrects for finite sample size (Burnham *et al.*, 2011). Model selection, averaging, and AICc weight calculation were performed using the package MuMin (Barton, 2014). Finally, to test the third aim,

comparing E₁C and PdG during pre- and post-conception swellings, I used two-tailed t-tests to compare log E₁C and PdG between post-conception swellings and published reports from non-conceptive and conceptive cycles.

4.3 Results

4.3.1 Aims 1 and 4: Variation in estrogen and progesterone production

E₁C concentrations vary tremendously among urine samples. Without controlling for gestation day or female ID, the average concentration among samples taken from fully swollen, pregnant females is 716.82 ng/ml, (range = 97.4 - 2983.37, n = 64). Among samples taken from nonswollen, pregnant females, the average concentration is slightly higher: 737.91 (range = 5.68-3866.01, n = 138), but this difference is not significant ($t = -1.6461$, $df = 200$, $p = 0.1014$), and likely due to the fact that estrogen is higher later in pregnancy when swellings are less common. Average PdG is 16.37 μ g/ml in nonswollen, pregnant females (range = 0.07 - 172.78, n = 159); in swollen, pregnant females, the average PdG concentration is 8.63 μ g/ml (range = 2.01 - 27.18, n = 74); these are significantly different ($t = 2.62$, $df = 231$, $p < 0.01$).

In order to specifically examine whether E₁C and PdG varied with age, I ran a LMM with hormone concentrations as outcome variables, controlling for trimester, swelling state, and pregnancy ID. Maternal age had no significant effect on E₁C in the full model ($p = 0.695$), and did not appear in either of the two best models after model selection. Instead, E₁C increased by trimester and was higher during full and partial swellings than on non-swollen days (Table 32). Marginal effects on E₁C production are illustrated in Figure 12.

Table 32: Factors influencing E₁C concentrations during pregnancy

Model	Intercept	Maternal Age	Trimester	Swelling	AICc	Delta	Weight
1	5.1201		0.2765		318.5014		0.6776
2	4.9156		0.3133	0.07914	319.9867	1.4853	0.3224
Average	5.0541		0.2884	0.0791			

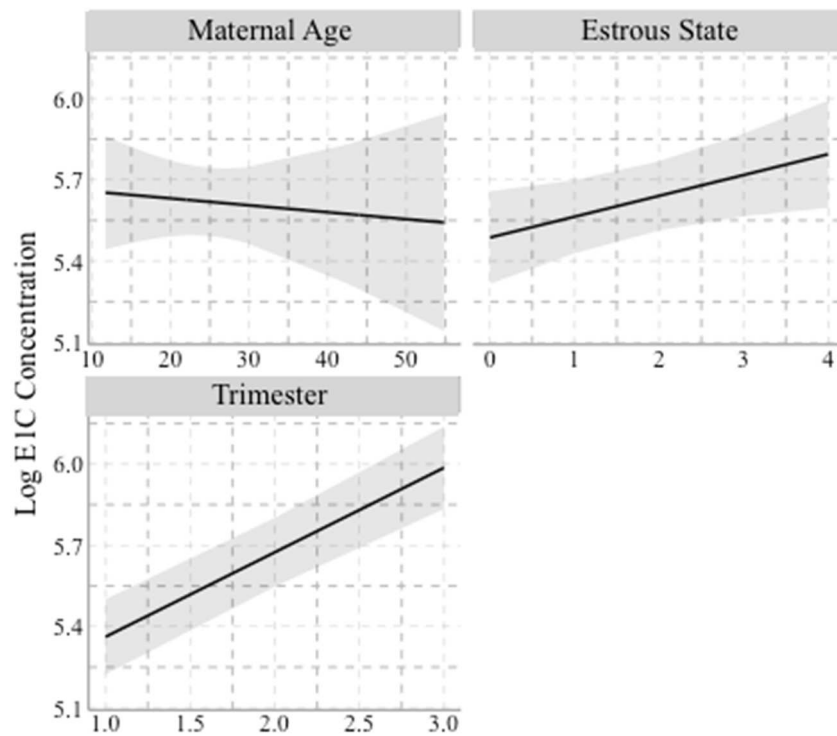


Figure 12: Marginal effects on E₁C concentrations during pregnancy. Clockwise from top left: Maternal age (years), estrous state (0 = no swelling, 3 = full swelling), and trimester. Predicted values are drawn from the full model. Shaded areas indicate 95% confidence intervals.

Similarly, PdG production during pregnancy is not significantly affected by age in the full model, although there was a trend toward lower PdG production in older females ($p = 0.0848$). Model selection yielded a single best model showing that trimester (1, 2, or 3) is the best predictor of PdG concentrations throughout gestation, and that PdG increases with successive trimesters (Table 33).

Table 33: Factors influencing PdG concentrations during pregnancy

Model	Intercept	Maternal Age	Trimester	Swelling State	AICc
1	3.6055		0.1763		287.7869

4.3.2 Aim 2: Hormonal effects on swelling during pregnancy

I tested the effects of E1C and PdG on estrous state during pregnancy, as described in the methods. Model selection using AICc yielded three best models (Table 34). In the average of these best models, E₁C had a positive effect on swelling (coefficient = 0.8503), while PdG was negatively correlated with swelling (coefficient = -0.1672). Swellings were also less likely in later trimesters, leading to a negative correlation between trimester and swelling (coefficient = -0.4929). Marginal effects of these predictors are illustrated in Figure 13.

Table 34: Factors influencing the presence of a sexual swelling during pregnancy

Model	Intercept	Log E1C	Log PdG	Trimester	AICc	Delta	Weight
1	-0.8666	0.7662	-1.7093		322.7635	0	0.4922
2	-0.1686	0.9798	-0.4929	-1.6885	323.5554	0.7919	0.3199
3	3.143			-1.544	324.7453	1.9818	0.1879
Average	0.1010	0.8503	-1.6715	-0.4929			

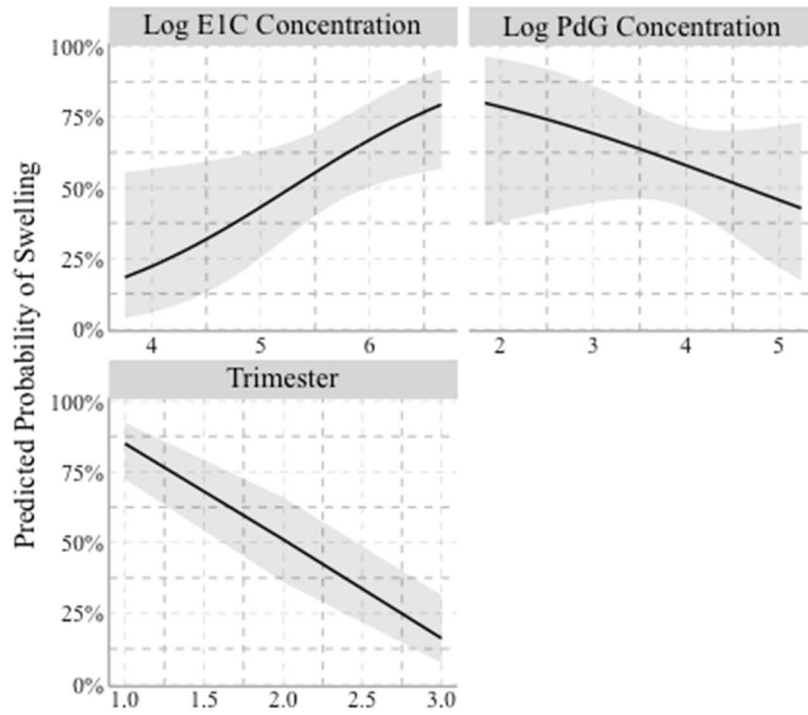


Figure 13: Marginal effects on swelling in pregnancy. Clockwise from top left: E₁C concentration (log pg/ml), PdG concentration (log µg/ml), and trimester. Predicted probabilities are drawn from the full model. Shaded areas indicate 95% confidence intervals.

4.3.3 Aim 3: Comparison of hormones in pre- and post-conception swellings

I compared average concentrations of E₁C and PdG during gestation to published values of these hormones during both non-conceptive and conceptive cycles. As mentioned above, the published values come from samples collected from cycling females by M. Emery Thompson during the same period as the samples analyzed in this study (Emery Thompson, 2005). Collection, processing, and assays are therefore identical. A summary of steroid hormone concentrations in nonconceptive, conceptive,

and postconceptive swellings, averaged in fully swollen and non-swollen periods, is given in Table 35.

Table 35: Log steroid hormone concentrations across pre- and post-conception swellings.

		Fully Swollen			Nonswollen		
		Average	St Dev	n	Average	St Dev	n
E1C	Nonconceptive	4.4909	0.2975	40	4.2055	0.4031	13
	Conceptive	4.7754	0.3334	10	4.6382	0.3258	4
	Postconceptive	5.65	0.43	64	5.57	0.61	138
PdG	Nonconceptive	2.5197	0.4640	40	2.9058	0.5665	13
	Conceptive	3.1225	0.3402	10	3.7299	0.3958	4
	Postconceptive	3.81	0.33	96	3.99	0.52	159

E₁C is significantly higher in fully swollen, pregnant females than in fully swollen, non-pregnant females, in both non-conceptive ($t = -14.9442$, $df = 102$, $p < 0.00001$) and conceptive ($t = -6.1369$, $df = 72$, $p < 0.00001$) cycles. Fully swollen, pregnant females also have significantly higher PdG than fully swollen, non-pregnant females during both non-conceptive ($t = -18.332$, $df = 134$, $p < 0.00001$) and conceptive ($t = -6.2528$, $df = 104$, $p < 0.00001$) cycles. These relationships are illustrated in Figure 14. Perhaps the more relevant comparison is between fully swollen, pregnant females, and peak PdG concentrations in non-pregnant females, which occur during the luteal phase. PdG is higher during post-conception swellings than in the luteal phase of non-conceptive ($t = -8.401$, $df = 107$, $p < 0.00001$) cycles, but is not significantly higher than in the luteal phase of conceptive cycles ($t = -0.4726$, $df = 98$, $p = 0.6376$).

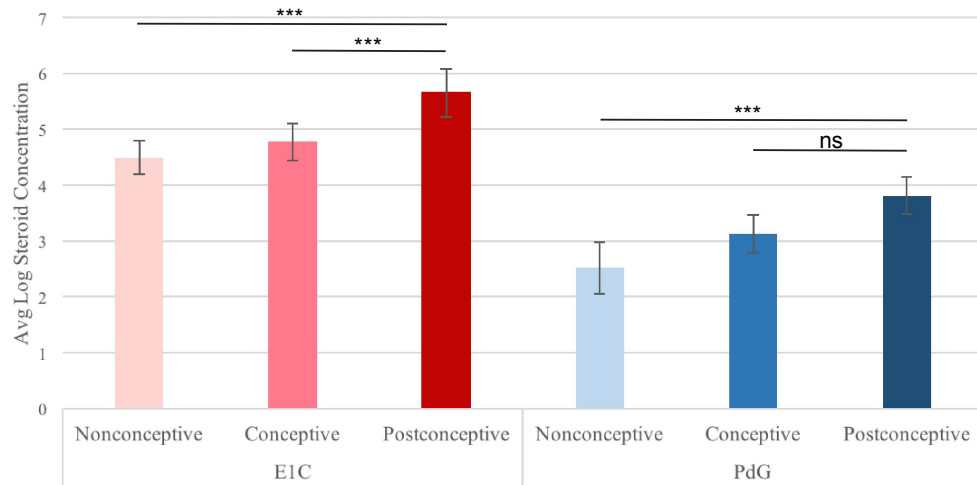


Figure 14: Average E₁C ng/ml and PdG µg/ml in fully swollen phases during nonconceptive, conceptive, and post-conceptive swellings. Error bars represent standard deviations.

4.4 Discussion

4.4.1 Summary of results

The first aim of this study was to determine how estrogen and progesterone concentrations change over gestation; I found that both increase significantly with successive trimesters, as predicted and previously documented in chimpanzees (Faiman et al., 1981; Shimizu et al., 2003). This rise is also typical of humans (Abbassi-Ghanavati et al., 2009) and other primate species (Solomon and Leung, 1972). The placenta is responsible for production of these steroid hormones during pregnancy, and produces them in such large quantities that the maternal ovaries are not necessary for maintenance of pregnancy after the first several weeks of pregnancy (Pasqualini and Chetrite, 2016).

Second, I asked whether the preconception relationships between estrogen, progesterone, and sexual swellings could be detected during pregnancy. Analysis of

urinary E₁C and PdG revealed that sexual swellings during pregnancy are governed by the same basic hormonal mechanism as those leading up to conception: Increased estrogen and decreased progesterone are associated with swelling during pregnancy. Given the known antagonistic effect progesterone on sexual swellings, it is surprising that they can occur in this high-progesterone milieu. However, the increase in estrogen associated with post-conception swellings may explain why males continue to mate with pregnant females. Recent research has indicated that males are sensitive to within-female and even within-cycle variation in swelling size, rather than absolute differences among females (Deschner et al., 2004; Emery Thompson and Wrangham, 2008). This sensitivity to slight changes in estrogen production allows them to mate during the most fertile days. It may also lead them to mate when pregnant females show a relative increase in estrogen, in spite of the complete lack of reproductive value of these matings.

Aim three was to characterize the differences between pre- and postconceptive swellings. In general, both hormones were elevated in pregnancy relative to nonconceptive and conceptive cycles alike. However, progesterone concentrations during swollen days in pregnancy were not significantly higher than luteal concentrations during conceptive swellings. On non-swollen days, progesterone is more than twice as high as in conceptive luteal phases. These findings suggest that decreased progesterone relative to baseline concentrations in pregnancy create a permissive environment for sexual swellings to occur. Working with captive chimpanzees, Faiman and colleagues (1981) showed that both serum estrogen and progesterone rise during pregnancy, but not at identical rates. As a result, there are periods, especially early in gestation, where estrogen

production outpaces progesterone production, leading to a positive ratio of E:P. Dahl (1999) reported that the timing of post-conception swellings aligned with these windows. However, swellings are by no means restricted to these windows, and occur much later into gestation than predicted by Faiman's periods of high E:P ratio (see Chapter 1).

In pursuit of Aim 4, to determine whether the effect of age on post-conception swellings is hormonally mediated, I found no significant effect of age on E₁C or PdG production. Differential sensitivity may be partially responsible for the observed effect of age, wherein younger females are more likely to exhibit post-conception swellings (Chapter 1). In captive chimpanzees, nulliparous females reached full tumescence at lower absolute levels of urinary estrone than did multiparous females, suggesting that their sexual skins were more highly sensitive to the effects of estrogen (Dahl et al., 1991). In Barbary macaques, post-conception estrus was fairly stereotyped, occurring ~18 days after the end of the conceptive cycles, but young adult females had the largest sexual swellings of any age group (Küster and Paul, 1984). Pregnancy in Guinea baboons (*P. papio*) is marked by flat, pink, sexual skins; however, in young females, the color of the sexual skin changes several times around conception before settling into the typical pink of pregnancy. This "color waltz," as it is dubbed by researchers, becomes less pronounced with successive pregnancies, which could also be evidence of reduced sensitivity in older females (Gauthier, 1999).

4.4.2 The role of the placenta and implications for the mechanism of selection on post-conception swellings.

Sexual swellings reflect the hormonal profile of female chimpanzees, and we can measure that profile through serum, fecal, and urinary sampling. None of these measures reveal the sources of steroid hormones during pregnancy, which may be critical to understanding selection on this maternal phenotype. Progesterone production is almost entirely placental after approximately six weeks of pregnancy; however, it likely uses maternal cholesterol and pregnenolone as precursors. Fetal androgens act as precursors to estrogen, and are aromatized in the placenta to produce E₁, E₂, and E₃. Maternal adrenal androgens are another source of precursors, but make up a much smaller portion of the pool (Faiman et al., 1981). Therefore, although selection for post-conception swelling appears to vary in response to maternal characteristics that make her more vulnerable to infanticide and intrasexual aggression, it must also be able to act on the fetal-placental unit (Pasqualini and Chetrite, 2016). Determining the pathways that connect maternal social environment to fetal androgen production is an important direction for future work on the adaptive significance of post-conception sexual swellings. The sources and effects of cortisol are particularly difficult to pinpoint during pregnancy, when maternal, fetal, and placental compartments all contribute to circulating concentrations (Pasqualini and Chetrite, 2016), but cortisol is a good candidate for the link between external effects acting on the female and fetal steroid production. Social stress has been demonstrated to affect glucocorticoid production in female chimpanzees (Emery Thompson et al., 2010). Perhaps the increased production of glucocorticoids in the adrenal glands, the source of precursors for placental steroid production, leads to elevated placental estrogen

production. This explanation is speculative at best, however, and would require more detailed assays of maternal and fetal adrenal activity in conjunction with data on sexual swellings before this potential link can be evaluated objectively.

5. Conclusions

Female chimpanzees face an array of serious threats to their own survival and reproductive success. They are limited by their ability to forage efficiently and maintain the energetic reserves necessary for reproductive function (Murray et al., 2009; Emery Thompson et al., 2010, 2014). Disease, predation, and injury threaten survival and fertility (Williams et al., 2008; Keele et al., 2009; Jones et al., 2010). However, their own conspecifics may present the greatest risk. Males commit infanticide and use aggressive sexual coercion to limit female promiscuity and mate choice (Takahata, 1985; Arcadi and Wrangham, 1999; Muller et al., 2009, 2011; Mjungu et al., 2014); females can also be aggressively competitive and infanticidal (Kahlenberg et al., 2008a; Pusey et al., 2008; Miller et al., 2013).

Behavioral adaptations to these threats are well documented. Females, especially mothers, are less gregarious than other individuals, and spend much of their time in the relative safety of solitude, avoiding both aggression and feeding competition (Otali and Gilchrist, 2006). Promiscuous mating itself is likely a counterstrategy to infanticide, allowing females to confuse paternity (van Schaik et al., 2000). Exaggerated sexual swellings facilitate promiscuous mating and paternity confusion by obscuring the exact timing of ovulation (Nunn, 1999; Deschner et al., 2004). In this dissertation, I presented evidence to show that sexual swellings during pregnancy represent another adaptation to extend sexual receptivity, reducing received aggression and lowering the risk of infanticide.

Females vary in the degree to which they are susceptible to infanticide and aggression from other females. I predicted that post-conception swellings could offer protection from both of these risks, and that between-female variation in the occurrence of post-conception swellings should reflect the variation in risk. I found evidence that young, low-ranking, and immigrant females swell more during pregnancy. In the first births of immigrant females, the extent of post-conception swelling is inversely related to their tenure in their adult community—more recent immigrants swell more during pregnancy, likely to extend the window of sexual receptivity and confuse paternity before giving birth. Unsurprisingly, given that females are more gregarious while in estrus, females with more post-conception swellings also have stronger overall associations with males during pregnancy.

These associations may carry their own benefits, although the signature of male sexual coercion is still clear: females associate more with those males who are more aggressive toward them; these males are also more likely to sire their offspring (Feldblum et al., 2014). However, females have stronger grooming relationships with males who are likely to offer protection to them, including their kin and the sires of their offspring. They do not groom more with the sires of their offspring before pregnancy, suggesting that they are able to identify the sire via an as-yet-unknown mechanism. This finding is part of an emerging body of evidence that paternity may be discernible even after promiscuous mating (Murray, in press). Finally, females with a strong grooming partner before and during pregnancy receive less aggression overall after giving birth. Mating

during pregnancy is also related to reduced aggression after birth: a benefit won through post-conception swellings, since females only mate while swollen.

Post-conception swellings have remained a puzzle in part because of the apparent conflict between the mechanism of sexual swellings and the typical hormonal profile of pregnancy. In Chapter 3, I showed that the same general relationships between estrogen, progesterone, and sexual swelling still hold during pregnancy: estrogen is higher and progesterone is lower on days with post-conception swellings. However, both of these hormones are vastly elevated relative to concentrations during preconception swellings. Younger females swell more during pregnancy than older females, but do not have absolutely higher concentrations of estrogen, suggesting that they may be more sensitive to its effects. The production of steroid hormones during pregnancy involves a complex set of interactions among the mother, fetus, and placenta. One fascinating question is how selection for extended sexual receptivity in females has acted on all three players. While this question remains unanswered, I have provided evidence in this dissertation that post-conception swellings are part of an adaptive response to sexual conflict in chimpanzees.

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Biography

Emily Boehm was born in Denver, Colorado, on February 9th, 1987. She attended Harvard University and graduated *cum laude* with a Bachelor of Arts in June, 2009. She entered the graduate program in Evolutionary Anthropology at Duke University in 2011 and was awarded the James B. Duke Fellowship. In 2013, she was awarded the Duke Sigma Xi Sally Hughes-Schrader Travel Grant in support of her field work in Gombe National Park, TZ. She was also awarded a Duke Summer Research Fellowship in 2016.