Reproduction, sexual swellings and mating behavior in Sanje mangabeys (*Cercocebus sanjei*)

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Abstract of the Dissertation

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Sexual selection theory predicts that, given the generally lower parental investment of mammalian, males should mate indiscriminately, while females should try to be selective, choosing high-quality mates to maximize their chances of offspring survival. Under certain circumstances, however, such as when females differ in fertility and/or sperm depletion may occur, males may become choosy mating partners, guarding and concentrating mating efforts on high-quality females. Similarly, when the risk of infanticide by males is high and females may benefit from parental care provided by putative fathers, females may mate promiscuously to confuse paternity while at the same time attempting to concentrate paternity in the highest quality male. As a result of this intersexual conflict with respect to reproductive goals, males and females have evolved evolutionary counterstrategies to help them implement their mating agenda at the expenses of the other sex. In primates, these counterstrategies include mate guarding by males, and long periods of sexual receptivity coupled with the development of exaggerated sexual swellings in females.

My study contributes to our current knowledge of sexual selection theory and inter-sexual conflict by examining reproduction, sexual swellings and mating behavior in wild Sanje mangabeys (*Cercocebus sanjei*), a species in which females develop an exaggerated sexual swelling during their menstrual cycle, as well as during gestation. My goals for this dissertation are: (1) to describe the ovarian endocrinology and reproductive characteristics of the Sanje mangabey; (2) to describe changes in the tumescence and appearance of the sexual swelling and how they relate to the timing of ovulation, female fertility and age-class; and (3) to examine what male Sanje mangabeys know about the timing of ovulation and female fertility. In particular, to determine if males are able identify the timing of ovulation, and if they use sexual swellings to assess when ovulation is most likely, as well as to distinguish between females of different fertility. As male rank may determine access to females, I also determine the male dominance hierarchy. My study was conducted on an habituated group of wild Sanje mangabeys over a 23-month period. Data collected include (1) demographic data on births, deaths, injuries and disappearance (N = 408 days); (2) sexual swelling tumescence and appearance using a visual scale specifically designed for this study; (3) fecal samples for the analysis of fecal estradiol and progesterone metabolites (N = 936 samples); (4) behavioral data on socio-sexual behavior through all-day female focal follows of one receptive female throughout her receptive period (N = 178 focal/days) to examine male interest in females; and (5) all occurrences of male agonistic interactions to determine the male dominance hierarchy (N = 408 days).

My results demonstrate that in Sanje mangabeys fluctuations of fecal estradiol (fE) during the menstrual cycle were comparable to those described in the related sooty mangabey.

They also displayed reproductive characteristics (i.e., menstrual cycle length, number of cycles to conception, gestation length and duration of post-partum amenorrhea) that were within the expected range compared to other cercopithecines. The exception was an earlier onset and longer duration of menstruation and implantation bleeding. Adolescent females displayed significantly longer menstrual cycles compared to adults, as well as a period of adolescent sterility, cycling for up to 16 months without conceiving. Both adults and adolescents exhibited extended periods of sexual receptivity, mating during non-fertile periods of their menstrual cycle and, for adults, also during gestation. Sexual swellings of Sanje mangabeys provided accurate information on the fE surge, used in this study as a proxy for ovulation. In particular, the fE surge only occurred when the swelling was at maximum tumescence. Moreover, within the period of maximum tumescence, the appearance of the swelling skin changed becoming a brighter color (hereafter 'the shiny phase'), which coincided with the fE surge, providing an even more precise signal of female fertility than tumescence alone. This is consistent with the graded-signal hypothesis to explain the function of sexual swellings in which the swelling is argued to indicate the most likely period of ovulation but not its exact timing. I found that different types of sexual swellings (i.e., first swelling post-partum, first swelling after infant death, swelling during adult non-conceptive and conceptive cycles, and post-conceptive swelling), and of females of different age-class (adult, adolescent), differed in maximum tumescence and/or shiny phase duration, which suggests that length of these phases may provide additional cues to the male regarding female fertility. In male Sanje mangabeys access to fertile females was influenced by dominance rank. During periods of female synchrony (i.e., more than one receptive female at a time), alpha males chose only one female to mate-guard, giving subordinate males access to mating opportunities with other swollen females. This conforms to the priority of access model. This pattern

disappeared during a period of rank instability after a new male had obtained the alpha position, during which time subordinate males obtained more mating access than dominant males. The alpha males exhibited greater interest in females during the fE surge compared to outside this period, during the start of the shiny phase – which coincided with the fE surge – compared to the rest of the shiny phase, and with females during the shiny phase compared to other swelling states, indicating that they prefer females during ovulation. They also preferred females that were undergoing conceptive cycles, over non-conceptive cycles and were less interested in females with post-conceptive swellings. This latter finding, however, may have been a consequence of the fact that the post-conceptive swellings included in this analysis did not reach maximum tumescence or display the shiny phase. Finally, the alpha male preferred adult over adolescent females.

My study contributes to the field of sexual selection theory by demonstrating the presence of inter-sexual conflict in Sanje mangabeys, as dominant males concentrated their mating efforts in the most fertile females, which they attempted to monopolize. Despite this, the sexual swellings and long receptive periods allowed females to overcome mate-guarding efforts and mate promiscuously with multiple males, while trying to concentrate paternity in the best male (i.e., mating during the fE surge with the male with the highest competitive ability). Future studies should examine paternity to assess how effective dominant males are at monopolizing matings with fertile females, the role of female behavior in male mating success, and whether females gain benefits in the form of paternal investment from putative fathers.

RESUMEN

La teoría de la selección sexual predice que, debido a que en mamíferos la inversión paterna es menor que la materna, los machos deben aparearse indiscriminadamente, mientras que las hembras deben ser selectivas y elegir machos de alta calidad para así maximizar las probabilidades de supervivencia de su progenie. Sin embargo, bajo ciertas condiciones, por ejemplo, cuando las hembras difieren en su fertilidad, o cuando el esperma es limitado, los machos deberían aparearse de manera más selectiva, concentrándose en las hembras más fértiles. Del mismo modo, cuando el riesgo de infanticidio es alto, y cuando las hembras se pueden beneficiar de la inversión paternal proporcionada por los padres putativos de las crías, las hembras, además de tratar de concentrar la paternidad en el macho con mejores cualidades, deberían aparearse promiscuamente para así confundir la paternidad entre los machos. Este conflicto intersexual, resultado de los diferentes objetivos reproductivos entre machos y hembra, ha provocado que ambos sexos hayan evolucionado una serie de rasgos que faciliten la implementación de sus propias estrategias reproductivas a costa de las estrategias del sexo opuesto. En primates, tales rasgos incluyen la monopolización de las hembras por parte de los machos, y largos periodos de receptividad sexual acompañados del desarrollo de hinchazones sexuales en las hembras.

El presente estudio examina la reproducción, los hinchazones sexuales y el apareamiento en un grupo en libertad de mangabeys de Sanje (*Cercocebus sanjei*), una especie de primate en el que las hembras desarrollan hinchazones sexuales durante el ciclo menstrual y la gestación. Los objetivos de este estudio son los siguientes: (1) describir la endocrinología y las características reproductivas del mangabey de Sanje; (2) describir los cambios en la tumescencia y la luminosidad del hinchazón sexual, y cómo tales cambios se relacionan con la ovulación, la

fertilidad y la edad de las hembras; y (3) examinar el posible conocimiento que los machos del mangabey de Sanje tienen a ese respecto. En concreto, el presente estudio investiga si los machos son capaces de identificar el periodo de ovulación, y si usan el hinchazón sexual para estimar cuándo es más probable que la hembra ovule, así como para distinguir entre hembras de distinta fertilidad. Debido a que en los machos el rango que ocupan en la jerarquía puede determinar al acceso a las hembras, este estudio también investiga la jerarquía entre los machos. El presente trabajo se realizó durante 23 meses en un grupo de mangabeys the Sanje habituado a la presencia humana. Durante dicho tiempo se recogieron datos en (1) la demografía del grupo, incluyendo nacimientos, muertes, heridas y desapariciones de los individuos (N = 408 días) y (2) la tumescencia y la luminosidad diaria de los hinchazones sexuales de todas las hembras, utilizando para ello una escala visual diseñada específicamente para éste estudio; (3) muestras fecales de todas las hembras adultas para el análisis de los niveles de los metabolitos de estradiol y progesterona en las heces (N = 936 muestras); (4) datos del comportamiento socio-sexual a través de seguimientos focales diarios de una hembra durante la duración de su periodo receptivo (N = 178 días focales), lo cual se usó para examinar el interés de los machos hacia las hembras; y (5) todos los casos observados de agresión entre los machos adultos, que sirvió para conocer su jerarquía (N = 408 días).

Los resultados del presente trabajo indican que las fluctuaciones de estradiol en las heces (fE) durante el ciclo menstrual son similares a las descritas en el mangabey gris (*C. atys*). Del mismo modo, el mangabey de Sanje muestra características reproductivas (duración del ciclo menstrual, número de ciclos hasta la concepción, duración de la gestación y duración la amenorrea lactacional) análogas a lo que se esperaría en función de lo que se ha descrito en otros cercopitecos. La única excepción fue el inicio temprano y la larga duración de la menstruación y del sangrado de implantación. Las hembras adolescentes mostraron ciclos menstruales significativamente más largos que los ciclos de las hembras adultas, así como un periodo de esterilidad durante el cual menstruaron hasta 16 meses consecutivos sin llegar a concebir. Tanto las hembras adultas como las adolescentes exhibieron largos periodos de receptividad sexual durante cada ciclo menstrual, apareándose durante periodos infértiles del ciclo y, en el caso de las adultas, también durante la gestación. Asimismo, este estudio ha encontrado que los hinchazones sexuales proporcionan información precisa sobre la elevación de fE, usado como indicador de la ovulación. En concreto, la elevación de fE se produjo exclusivamente cuando el hinchazón se encontraba en el periodo de máxima tumescencia. Es más, durante este tiempo de máxima tumescencia, la luminosidad del hinchazón cambia y adquiere un tono más brillante (referido a partir de ahora como “fase brillante”), el cual coincide con la elevación de fE. Dicho cambio en luminosidad proporcionó a los machos una señal aún más precisa que la tumescencia respecto a la fertilidad de la hembra. Estos resultados son consistentes con la “hipótesis de la señal gradual” propuesta para tratar de explicar la función de los hinchazones sexuales. Dicha hipótesis establece que los hinchazones indican el momento más probable de ovulación pero sin llegar a indicarlo concretamente. Los resultados de esta investigación también han revelado que diferentes tipos de hinchazones sexuales, esto es, el primer hinchazón después del parto, el primer hinchazón tras la muerte de una cría, el hinchazón durante un ciclo menstrual en el que no hay concepción, y el hinchazón durante el ciclo en el que la hembra concibe; así como hinchazones de hembras de diferente edad, en concreto adultas y adolescentes; difieren en la duración del periodo de tumescencia máxima y/o la duración de la fase brillante del hinchazón. Dichos resultados sugieren que la duración de estos periodos podrían proporcionar a los machos información adicional sobre la fertilidad de las hembras. Por otra parte, en los machos del mangabey de Sanje, el rango en la jerarquía determinó el acceso a las hembras. Así mismo, durante periodos en los que hay más de una hembra receptiva, el macho alfa trató de monopolizar una sola hembra, lo cual proporcionó a los machos subordinados la oportunidad de aparearse con otras hembras. Tal comportamiento, el cual corresponde con el "modelo de acceso prioritario", despareció durante un periodo de inestabilidad en la jerarquía que siguió al derrocamiento del macho alfa por parte de un nuevo macho. Durante este periodo de inestabilidad, los machos subordinados acapararon una proporción de los apareamiento mayor que la del macho alfa. Ambos machos alfa mostraron mayor interés en las hembras durante el periodo de elevación de fE respecto a otras partes del ciclo, así como en hembras durante el comienzo de la fase brillante (el cual coincide con el periodo de elevación de fE) en relación con el resto de la fase brillante, y en hembras durante la fase brillante comparado con otros estados del hinchazón sexual. Tales resultados indican que los machos están más interesados en las hembras durante el periodo de ovulación. Del mismo modo, los machos alfa mostraron mayor interés en las hembras durante los ciclos en los que concibieron, comparado con ciclos en los que no hubo concepción; mientras que el menor interés lo mostraron hacia hembras durante hinchazones sexuales desarrollados durante el embarazo. Este último resultado, sin embargo, podría estar debido a que ninguno de los hinchazones durante el embarazo utilizados en el análisis alcanzaron el periodo de máxima tumescencia y la fase brillante. Finalmente, los machos alfa prefirieron a hembras adultas antes que las adolescentes.

El presente estudio contribuye al campo de la selección sexual al demostrar la presencia de conflicto intersexual en el mangabey de Sanje, ya que los machos dominantes concentraron sus apareamientos en las hembras más fértiles, al tiempo que trataron de monopolizarlas. A pesar de ello, los hinchazones sexuales, así como los largos periodos de receptividad sexual, permitieron a las hembras superar los esfuerzos de los machos dominantes por monopolizar a las hembras y lograron aparearse promiscuamente con varios machos, al tiempo que concentraron la paternidad en el mejor macho al aparearse con el macho de mayor habilidad competitiva durante el periodo de elevación de fE. Futuros estudios deberán examinar la paternidad de las crías para establecer cuán efectivos son los esfuerzos de los machos por monopolizar a las hembras, la importancia del comportamiento de las hembras en el éxito de apareamiento de los machos, así como si las hembras reciben beneficios en forma de inversión paternal de los padres putativos de sus crías.

DEDICATION

To my parents and my sister for their unlimited support

&

to Gráinne, for being my rock

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CHAPTER ONE:

INTRODUCTION

Mating strategies of male and female primates

Darwin defined sexual selection as selection that ‘depends on the advantage which certain individuals have over others of the same sex and species, solely in respect of reproduction’ (Darwin, 1871, p 209). He also noted that the sexual behavior of males and of females appeared to be consistent across species, arguing that males mated indiscriminately, while females were passive but choosy sexual partners. These ‘classic’ sex roles of males and females were later reinforced by Bateman’s experiments with *Drosophila melanogaster* (Bateman, 1948), whereby he explained that mating variance was much higher in males compared to females due to males’ indiscriminate mating and females’ passivity. It was Trivers (1972), however, who successfully explained the force behind these specific sex roles; i.e., the differential reproductive investment of males and females. In particular, males’ investment is generally small (i.e., sperm) compared to females’ (i.e., large ova, gestation, lactation). This difference in parental investment is particularly pronounced in mammals, including anthropoid primates. In such species, females typically give birth to a single offspring after a gestation period of six to nine months, followed by a lengthy period of lactation and post-partum amenorrhea (Harvey et al., 1987), while males generally have limited involvement in infant care. Males, therefore, should be selected to mate indiscriminately because their reproductive success is highly dependent on access to the limited number of available fertile females, whereas females would benefit by being choosy with respect to mating partners to ensure the best males sire and pass on their genes to their potentially few, but more costly offspring.

Today, studies from most primate taxa have demonstrated that the traditional sex roles of indiscriminate males and choosy females do not entirely encompass what we observe in nature: Males, on many occasions, can also be choosy mating partners, targeting specific females in which they concentrate most of their mating effort, while ignoring others. This is likely due to the fact that sperm is not an unlimited resource (Small, 1988), contrary to what has been traditionally thought, as frequent ejaculations can decrease sperm count per ejaculate and affect the chances of fertilization (Dewsbury, 1982; Marson et al., 1989; Preston et al., 2001; Thomsen et al., 2006). For example, in feral Soay sheep (*Ovis aries*), dominant males sire fewer lambs as the rutting season progresses, despite maintaining a constant copulation frequency (Preston et al., 2001). Similarly, rather than being coy, passive or choosy, females have been found to be active, ardent, promiscuous sexual partners (Hrdy, 1977; reviewed in Gowaty, 2004). There are several possible reasons for this behavior. First, males may differ in their quality as mates; thus, females may choose a partner who will provide the greatest genetic or social benefits to herself and her offspring (Cashdan, 1996). In wild savannah baboons (*Papio cynocephalus*), for example, fathers are more likely to support their infants in agonistic encounters, and their presence enhances growth and development of their offspring (Buchan et al., 2003; Charpentier et al., 2008). Second, promiscuous mating may confuse paternity, providing benefits to females by gaining additional investment from non-paternal male mating partners, such as protection for herself and her infant (Taub, 1980; Hrdy, 1981; van Noordwijk, 1985; Harvey and May, 1989; Palombit et al., 1997; Borries et al., 1999). Finally, in species where the risk of infanticide is high, confusing paternity may also prevent new dominant males from killing infants (Hrdy, 1977) . Thus, females are faced with what has been referred to as the ‘female dilemma’ (van Schaik et al., 2001), that is, they should try to concentrate paternity in the best male, while confusing paternity among other resident males, in order to accrue these additional benefits of paternal care and reduced risk of infanticide (Hrdy and Whitten, 1987).

Given the differential reproductive goals of male and female primates, it follows that their mating interests would collide, as males try to monopolize quality females, while females attempt to mate with several males. This forms the basis of inter-sexual conflict (Parker, 1979; Chapman et al., 2003), which in recent years has grown in recognition as a major force affecting the evolution of behavioral, anatomical, physiological and genomic primate traits (van Schaik et al., 2004; Muller and Wrangham, 2009; reviewed in Stumpf et al., 2011). In addition, given that inter-sexual conflict can affect the mating system and social dynamics within the group, it has become one of the central tenants of sexual selection theory and a primary structural factor in current models of social organization (Parker, 1979; Hammerstein and Parker, 1987; van Schaik, 1996; Sterck, 1997; Gowaty, 2004; van Schaik et al., 2004).

Male mating strategies: guarding fertile females

As a result of the evolutionary arms-race, males and females have evolved traits that enable them to gain an advantage over the opposite sex and implement their reproductive goals at the other's expense (Dawkins and Krebs, 1979; Clarke et al., 2009a). For males in species with large sexual dimorphism one such behavioral trait is the harassment of females that includes forcing them to mate (Smuts and Smuts, 1993; Muller and Wrangham, 2009). In extreme cases, males may even kill the female's infant, as this results in the resumption of cycling, increasing the number of available fertile females (Hrdy, 1977; 1979; van Schaik and Janson, 2000). The most common male strategy in multi-male groups of such male coercion is mate-guarding, whereby individuals with the highest competitive ability (i.e., highest rank) prevent others from mating with the female he is guarding, thereby monopolizing most copulations (reviewed in

Dixson, 2012). Accordingly, in most cases male rank correlates with mating success, which usually translates into higher reproductive success (e.g., Dixson et al., 1993; de Ruiter et al., 1994; Altmann et al., 1996; Brauch et al., 2008). When there are several receptive females at the same time, however, the alpha male is not capable of complete mating monopolization (Say et al., 2001; Takahashi, 2004) and, instead must choose among females. In this case, dominant males are predicted to concentrate their guarding and mating effort in the most fertile female; i.e., the female that is closest to ovulation, in order to maximize their reproductive success (Packer, 1979; Alberts et al., 1996; Wedell et al., 2002), provided the male is capable of detecting ovulation.

The degree to which males are able to detect ovulation appears to vary among species. For example, in Assamese macaques (*Macaca assamensis*), most ejaculatory copulations (89%) by dominant males were outside the fertile phase of the cycle, and most females (60%, 9 of 15) were not observed to be consorted by – although they mated with – males around the most probable conception period, which suggest that males were not able to detect ovulation (Fürtbauer et al., 2011). Similarly, a wild western gorilla (*Gorilla gorilla*) silverback, at times when there were a pregnant and a cycling female sexually receptive, mated with both, which suggests that he lacked the ability to detect ovulation (Doran-Sheehy et al., 2009). Conversely, in other species, males prefer females with the largest sexual swellings as mating partners (e.g., savannah baboons, *P. ursinus*: Bulger, 1993; Mandrills, *Mandrillus sphinx*: Setchell et al., 2005), which typically coincides with ovulation (Dixson, 1983). Finally, it has been argued that some species are able to pinpoint the exact timing of ovulation (chimpanzees, *Pan troglodytes verus*: Deschner et al., 2004; Barbary macaques, *M. sylvanus*: Heistermann et al., 2007; olive baboons: *P. hamadryas anubis*: Daspre et al., 2009; Higham et al., 2009; Sulawesi macaques, *M. nigra*: Higham et al. 2012). Additional evidence indicates that males may be able differentiate among females of different reproductive quality, preferring females that are undergoing conceptive versus non-conceptive cycles (savannah baboons: Bulger, 1993; Weingrill et al., 2003; Gesquiere et al., 2007), or females of higher versus lower rank (Mandrills: Setchell and Wickings, 2006), which has been shown to translate into higher reproductive success in some taxa (callitrichids Abbott, 1993; East African chimpanzees, *P. t. schweinfurthii*: Pusey et al., 1997; reviewed in Harcourt, 1987); females of mature age versus those that are younger (Chimpanzees: *P. troglodytes*: Muller et al., 2006), and cycling versus pregnant females (Barbary macaques: Küster and Paul, 1984; Gordon et al., 1991; sooty mangabeys: *Cercocebus atys*: Gust, 1994).

Female counterstrategies: long receptivity, promiscuity and sexual swellings

Several female counterstrategies to male mating behavior have been identified among primates. These include extended receptive periods (i.e., a time of increased frequency of behaviors that facilitate copulations [Hrdy and Whitten, 1987]), coupled with promiscuous mating and the development of exaggerated sexual swellings. Each of these is suggested to improve the ability of females to implement their own reproductive agenda in the face of what appears to be restrictive male mating behavior (Nunn, 1999a; van Schaik et al., 2000).

Prolonged periods of sexual receptivity are characteristic of many female primates. During such periods, females can be observed mating during non-fertile days of the sexual cycle, rather than exclusively during ovulation which is more common among other mammals (Heape, 1900). Among primates, such behavior is more frequently found in cercopithecines living in multi-male groups, where females display follicular phases (i.e., the portion of the menstrual cycle that ends with ovulation and when most sexual behavior occurs) that are longer compared to other primate radiations (van Schaik et al., 2000). Longer periods of receptivity may increase the probability of reproductive synchrony with other females (Nunn, 1999a). Reproductive synchrony will, in turn, reduce male mating skew; i.e., the unequal distribution of copulations across males. This would give females the opportunity to mate with additional males, other than the alpha who may otherwise have tried to exclusively guard her (i.e., priority of access model, Altmann, 1962), and thus, confuse paternity. The ability to confuse paternity may be particularly adaptive in species that have prolonged periods of lactational amenorrhea compared to gestation, and do not exhibit post-partum mating, two traits that have been linked to increased infanticide risk in primates (van Schaik, 2000; van Schaik et al., 2000). Female primates may also engage in non-conceptive mating. For example, some species mate during gestation (e.g., Gust, 1994; Soltis et al., 1999; Engelhardt et al., 2007; Doran-Sheehy et al., 2009; Fürtbauer et al., 2011; Lu et al., 2012), which has been argued by some to function to further confuse paternity (Hrdy, 1974; Taub, 1980).

One of the most conspicuous female counterstrategies may be the development of exaggerated sexual swellings, an enlargement of the perineal area that becomes tumescent during the period of sexual receptivity, peaking in size around the time of ovulation (Dixson, 1983). Sexual swellings are found in multiple species of catarrhine primates, and are argued to have evolved at least three separate times, in cercopithecines, African colobines and apes (Nunn, 1999a). There are several hypotheses to explain the function and evolution of such swellings (the best-male hypothesis: Clutton-Brock and Harvey, 1976; the many-male hypothesis: Hrdy, 1981; Hrdy and Whitten, 1987; the obvious-ovulation hypothesis: Hamilton, 1984; the male services hypothesis: van Noordwijk, 1985; the reliable indicator hypothesis: Pagel, 1994; the graded-signal hypothesis: Nunn, 1999a; the differentiating between cycles hypothesis: Zinner et al., 2002; Emery and Whitten, 2003; the paternal care hypothesis: Alberts and Fitzpatrick, 2012; see Alberts and Fitzpatrick 2012 for a review). Each of these hypotheses addresses a different level of variation in sexual swelling size: variation within a cycle, variation between cycles of the same female, and variation between swellings of different females (Alberts and Fitzpatrick, 2012). Accordingly, these three levels of variation correspond to three different types of information that sexual swellings may convey: the timing of ovulation, differences in fertility (e.g., probability of conception) of consecutive cycles of the same female, and differences in quality (e.g., physical condition) among females, respectively (Alberts and Fitzpatrick, 2012).

The hypothesis that has received the most support to date is the graded signal hypothesis, which examines variation in size within a single cycle and suggests that swellings function as a probabilistic signal, indicating when ovulation is most likely but not its exact timing (Nunn, 1999a). According to this hypothesis, inter-sexual conflict is the main driver behind the evolution of sexual swellings (Nunn, 1999a; Zinner et al., 2004). This was proposed because of several factors, including that ovulation tends to occur when the swelling is largest, that sexual swellings are more common in species that live in multi-male mating systems, particularly those that are non-seasonal breeders, and where mating synchrony is expected to be lower, and therefore, it is more likely that males would be able to monopolize females during receptive periods. The graded signal hypothesis, therefore, states that sexual swellings should enable females to overcome the female dilemma by first concentrating paternity among the males with the most competitive ability (presumably the best males). These are the males that are more likely to be able to guard and mate with females when the swelling is largest (i.e., the probability of ovulation is highest). Accordingly, males compete more intensely over females when they are swollen (Dixson, 1983), and dominant males have preferential access to females during the time of maximum swelling (Nunn, 1999a; Alberts et al., 2003; 2006; but see Bissonnette et al., 2011). At the same time, extended periods of swelling would enable females to confuse paternity among the subordinate males, by providing opportunities for mating outside the period of maximum swelling, when the probability of ovulation is lower. As such, in a study of chacma baboons (*P. h. ursinus*), females solicited and mated with all males, irrespective of rank, which the authors argued was a strategy to confuse paternity and attain additional paternal support (Clarke et al., 2009b).

Further evidence that sexual swellings serve to confuse paternity can be found in 'deceptive' sexual swellings (Takahata et al., 1998), such as those developed by female hamadryas baboons shortly after male take-overs (Colmenares and Gomendio, 1988; Swedell, 2000; Zinner and Deschner, 2000). Females were observed mating while exhibiting these swellings, which were morphologically indistinguishable from regular swellings, but did not typically conceive. Given that these swellings caused females to significantly reduce their post-partum amenorrhea, but not their inter-birth interval, the authors concluded that such deceptive swellings functioned to confuse paternity and reduce the risk of infanticide by new dominant males (Zinner and Deschner, 2000).

Thus, evidence from most studies suggests that in cercopithecine primates inter-sexual conflict forms the basis male and female relationships, as they compete with each other to implement their own mating strategies; i.e., males aim to monopolize copulations while females' goal is to mate selectively during peak fertility, and promiscuously outside this period. The extent to which each sex is successful depends on social (e.g., male rank) and ecological factors (e.g., reproductive synchrony driven by seasonality). The outcome of this competition, however, has direct effects on the individual's reproductive success, and therefore, can have important evolutionary consequences. In spite of that, inter-sexual conflict has only recently been considered in primate studies as an explanatory framework, and current socio-ecological models fail to incorporate most forms of inter-sexual conflict affecting male and female relationships (Sterck et al., 1997).

The goal of this dissertation, therefore, is to contribute to our understanding of sexual selection theory and inter-sexual conflict by examining reproduction, sexual swellings and mating behavior in wild Sanje mangabeys (*Cercocebus sanjei*). Most previous research on primate inter-sexual conflict has focused on baboons, macaques and chimpanzees. This dissertation will broaden our knowledge by examining this issue in the genus *Cercocebus*. In addition, given that *Cercocebus* is phylogenetically closer to *Mandrillus* (mandrills and drills) than to baboons (Groves, 2001), this study provides a unique comparative insight into mating strategies and their effect on the evolution of cercopithecine social organization (Di Fiore and Rendall, 1994; Kappeler and van Schaik, 2002; Fuentes, 2007).

Inter-sexual conflict is predicted to be most intense in species with a multi-male, multi-female social system, and in particular, in species with a high operational sex ratio (i.e., a large number of sexually receptive females per male), where individuals form strong dominance hierarchies and there is high mating competition (Stumpf et al., 2011). Sanje mangabeys show a female-biased sex ratio, with up to four adult females per male (Ehardt et al., 2005). In addition, females develop an exaggerated sexual swelling during their menstrual cycles and during gestation, and long periods of sexual receptivity, as well as a peak conceptive season (McCabe, 2012), which increases the likelihood of reproductive synchrony (Nunn, 1999b). Also, during their receptive period, female Sanje mangabeys mate promiscuously (Ehardt and Butynski, 2013). Finally, males in a closely related species, *C. atys,* form a dominance hierarchy, competing for access to fertile females, whom they guard from other males (Gust and Gordon, 1991; Range et al., 2007), and thus it is likely that Sanje mangabey males do as well, although this has yet to be confirmed. The Sanje mangabey, therefore, represents an ideal species in which to examine inter-sexual conflict.

In this dissertation I will describe the ovarian endocrinology and reproductive characteristics of the Sanje mangabey, providing data that are limited for this genus, and completely lacking for this species. I will also describe changes in the tumescence and appearance of the sexual swelling relative to the timing of ovulation, female fertility, and female age class. Finally, I will examine male interest in females during their receptive period. Therefore, the specific aims of this dissertation are to first examine whether sexual swellings vary among females of differing fertility (i.e., first cycle post-partum versus later cycles, conceptive versus non-conceptive cycles, cycling versus pregnant, and in adult versus adolescent females), thereby providing visual signals of fertility to the male. Next, I examine the degree to which sexual swellings provide accurate information about the likelihood of ovulation, once again providing an accurate signal of cycle quality. Finally, I examine male behavior to determine whether males show greater interest in females during ovulation, and if so, is it on the basis of sexual swellings. These questions are addressed in chapters two through four, written in manuscript format and aimed to be published as individual papers in scientific journals.

The Sanje mangabey

The Sanje mangabey (*Cercocebus sanjei*) was first described in 1981 (Homewood and Rodgers, 1981). The species, listed as Endangered by the IUCN (Ehardt et al. 2008), is endemic to the Udzungwa Mountains of south-central Tanzania, part of the Eastern Afromontane Biodiversity Hotspot (Mittermeier et al., 2004). Its population, estimated between 1,300 and 3,500 individuals (Ehardt et al., 2005; Rovero et al., 2009), is limited to two isolated forest blocks of the Udzungwa Mountains: the Mwanihana Forest, within the Udzungwa Mountains National Park, and the Udzungwa Scarp Forest Reserve. These forests also harbor four other species of diurnal monkeys: the black and white colobus (*Colobus angolensis palliatus*), the Udzungwa red colobus (*Procolobus gordonorum*), the Sykes' monkey (*Cercopithecus mitis* cf. *monoides/moloneyi*) and the yellow baboon (*P. cynocephalus*) (Ehardt et al., 2005; Rovero et al., 2009). Sanje mangabeys live in multi-male, multi-female social groups, characterized by female philopatry and male dispersal (Ehardt et al., 2005; Ehardt and Butynski, 2013). They are arboreal, although they spend over 50% of their time foraging on the ground and in the lower canopy (Ehardt et al., 2005; Ehardt and Butynski, 2013). They have a highly omnivorous diet, consuming over 76 different species of plants, as well as fungi, insects and small vertebrates (Ehardt et al., 2005; McCabe, 2012; Ehardt and Butynski, 2013).

This research was conducted on the Mizimu group, within the Mwanihana Forest, first habituated by Ehardt and colleagues in 2004 and continuously monitored ever since (Ehardt et al., 2005; Ehardt, pers. comm.). Their home range of ~200 ha (Ehardt et al., 2005) overlaps with at least three other Sanje mangabey groups (Fernández, unpublished). During the study, the Mizimu group consisted of 63 to 65 individuals, including seven to ten adult males, 18 to 20 adult females, and their offspring. At the beginning of the study, I identified all adult members of the group using scars and facial coloration. Over the course of the study three females matured, and exhibited their first sexual swelling; thus, they were classified as adolescents. They were further distinguished from adult females by their relatively larger and brighter sexual swellings (Anderson and Bielert, 1994), as well as their button-like nipples (Altmann et al., 1977) and smaller body sizes (Sigg et al., 1982).

Overview of Thesis Chapters

In order to investigate the reproductive characteristics and mating behavior of the Sanje mangabey I have divided my study into three main questions, which correspond to each of the three research chapters of this dissertation. Each chapter will build upon the results of the previous chapters. In the following section I present a brief introduction and the main goals of each chapter.

Chapter two

In the second chapter (first manuscript), entitled '**Reproductive characteristics of wild Sanje mangabeys (*Cercocebus sanjei*)**' I examine the reproductive characteristics and ovarian endocrinology of female Sanje mangabeys. Currently, the majority of such information available for primate species is derived from captive or semi-captive populations (Martin, 2007; Dixson, 2012). Given the positive impact that a nutrient-rich diet can have on reproduction (Ellison, 2003; Altmann and Alberts, 2005), results derived from captive or semi-captive studies tend to overestimate the species' reproductive rates; thus, they do not accurately reflect the reproductive variation found in natural settings. This is particularly true for mangabeys of the genus *Cercocebus*, where limited reproductive data are available for three of the four to six *Cercocebus* species currently recognized; i.e., from captive studies of sooty mangabeys (*C. atys*) and golden-bellied (*C. agilis chrysogaster*) mangabeys (Hadidian and Bernstein, 1979; Calle et al., 1990; Gordon et al., 1991; Whitten and Russell, 1996; Walker et al., 2004) and from studies of wild Tana River (*C. galeritus*) and sooty mangabeys (Homewood, 1975; Kinnaird, 1990; Range et al., 2007). The goals of this chapter are 1) to provide baseline data on the reproductive biology of Sanje mangabeys including their ovarian endocrinology, as well as the following basic reproductive parameters: length of the menstrual cycle, number of cycles to conception, gestation length and duration of post-partum amenorrhea; and 2) to compare the endocrinology and reproductive parameters of the Sanje mangabey with other cercopithecine primates.

This chapter was written in collaboration with Dr. Diane Doran-Sheehy, Dr. Carola Borries and Dr. Janine L. Brown.

Chapter three

In the third chapter (second manuscript), entitled '**Sexual swellings of wild Sanje mangabeys (*Cercocebus sanjei*): Changes in tumescence and appearance in relation to swelling type, female age, and the timing of ovulation**' I describe the sexual swellings of Sanje mangabeys and attempt to determine their functional significance. As in many other cercopithecines, Sanje mangabey females exhibit exaggerated sexual swellings, a tumescence of the ano-genital skin that peaks in size around the time of ovulation (Dixson, 1983). They also develop a sexual swelling during gestation (i.e., a post-conceptive swelling).

The main goals of this chapter are to 1) describe the changes in tumescence and appearance of the sexual swelling during the menstrual cycle and during gestation; 2) examine how changes in tumescence and appearance relate to the timing of ovulation, testing whether the changes in sexual swellings have the potential to convey information about ovulation to males, consistent with the graded-signal hypothesis (Nunn, 1999a); and 3) compare whether sexual swelling tumescence and appearance vary among females of differing potential for fertilization (i.e., first swelling post-partum, first swelling after infant death, swelling during non-conceptive and conceptive cycles, post-conceptive swelling) and of swellings from females in different age-classes (adult, adolescent), thereby providing visual cues to males regarding differential fertility.

This chapter was written in collaboration with Dr. Diane Doran-Sheehy, Dr. Carola Borries, and Dr. Carolyn L. Ehardt.

Chapter four

The fourth chapter (manuscript three), entitled '**Male mating behavior in relation to ovulation, sexual swellings and female fertility in Sanje mangabeys'** builds upon the previous chapters to examine what male Sanje mangabeys may know about the timing of ovulation and female fertility. Male reproductive success is limited by access to fertile females (Trivers, 1972). In many primates, it is male rank that determines this access, such that the dominant male is able to monopolize most copulations. When females exhibit reproductive synchrony, as has been observed in the Sanje mangabey, the dominant male is not able to guard all available females and should concentrate his attention on the female that is closest to ovulation. This provides subordinate males with an opportunity to gain access to females that might otherwise not be available without reproductive synchrony (i.e., priority of access model: Altmann, 1962).

Detecting ovulation is hindered in primates compared to other mammals, as females will mate for prolonged periods, including outside of ovulation and during gestation (reviewed in Dixson, 2012). Despite this, some studies have shown that, in species with sexual swellings, males seem capable of distinguishing the timing of ovulation, as they showed greater mating interest towards females during this time (Deschner et al., 2004; Heistermann et al., 2007; Daspre et al., 2009; Higham et al., 2009; 2012). Furthermore, some males seem to be able to distinguish among synchronous females that are undergoing cycles of different reproductive quality or differ in fertility. For example, male baboons (Bulger, 1993; Weingrill et al., 2003; Gesquiere et al., 2007) and sooty mangabeys (Gordon et al., 1991; Gust, 1994) appear to prefer females undergoing conceptive cycles compared to those in non-conceptive cycles, and similar results have also been reported in other species (Barbary macaques: Küster and Paul, 1984). It has also been observed that males of some species prefer adults over adolescent females (reviewed in Anderson and Bielert, 1994), who typically undergo a period of adolescent sterility before conceiving (Hartman, 1931).

In this chapter, therefore, I 1) examine if males have a dominance hierarchy that determines mating access to females as predicted by the priority of access model; 2) investigate if males prefer females during ovulation by examining how their socio-sexual behavior towards receptive females changes relative to the timing of ovulation and to changes in the tumescence and appearance of the sexual swelling; and 3) investigate if male mating interests vary towards females of different fertility (menstrual non-conceptive, conceptive, post-conceptive cycles) and of different age-class (adults, adolescents). If male rank is a controlling factor in mating access for Sanje mangabeys, the behavior of the alpha male will be most informative in determining male preference, as their behavior will be the least constrained by male-male competition.

Chapter five

In chapter five, I provide a general summary of the results of this dissertation and discuss how they fit within our current knowledge of sexual selection theory. I also provide a synthesis of questions raised by the results of the study, future work that may further our knowledge of reproduction and mating behavior in *Cercocebus* mangabeys and a discussion of the significance of this dissertation to the field of sexual selection theory and primate behavior.

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CHAPTER TWO:

REPRODUCTIVE CHARACTERISTICS OF WILD SANJE MANGABEYS (*CERCOCEBUS SANJEI*)

*To be submitted under the title 'Reproductive characteristics of wild Sanje mangabeys (*Cercocebus sanjei*)' by David Fernández, Diane Doran-Sheehy, Carola Borries, and Janine L. Brown.*

Abstract

A basic understanding of reproductive characteristics and ovarian endocrinology is necessary to address fundamental questions about the reproductive strategies and life history of a species. For most primates, the majority of available data are derived from captive populations; however, due to the better quality diets of captive animals, information from such populations might not reflect the variation found in natural settings. Here we used analysis of fecal estradiol (fE) and behavioral observations to present the first data on the reproductive characteristics and endocrinology of a wild group (N = 18 adult females, 3 adolescent females) of Sanje mangabeys (*Cercocebus sanjei*), a primate with exaggerated sexual swellings. The study was conducted in the Udzungwa Mountains National Park, Tanzania, from October 2008 through July 2010. Average cycle length (± SD) calculated using menses was 30.0 ± 3.0 days in adults and 49.0 ± 6.3 days in adolescent females. Menses appeared within 5.7 ± 2.8 days in adults and 4.8 ± 0.5 days in adolescents relative to the end of maximum tumescence, and lasted 6.6 ± 2.6 and 9.2 ± 5.6 days in adults and adolescents, respectively. In all cycles for which there were hormonal data (adults: N = 9; adolescents: N = 3), average concentration of fE peaked when the sexual swelling was at maximum tumescence. Fecal progesterone showed high fluctuations during the cycle and could not be used for the detection of ovulation. Adult females underwent an average of 3.1 ± 1.6 cycles to conception. Females that lost an infant conceived faster (2.5 ± 1.3 cycles) compared to females with a surviving offspring (4.3 ± 1.5 cycles). Adolescent females exhibited a period of sterility and did not conceive within the first 16 months of cycling. After conception, implantation bleeding began 17.5 ± 0.7 days from the onset of detumescence, and lasted 10.0 ± 1.4 days. Mean gestation length was 171.8 ± 3.4 days, with fE levels increasing steadily throughout gestation, showing a significant increase during the second trimester and a further surge two weeks before birth. Fecal progesterone also increased throughout gestation, showing a six-week long surge from week 15 through week 10 prior to birth. The average period of post-partum amenorrhea lasted 6.7 ± 2.3 months after a surviving infant. Females whose infants had died resumed cycling 14.3 ± 5.9 days after infant death. Sanje mangabeys showed fE fluctuations during the menstrual cycle that resembled those of other mangabeys. Reproductive characteristics were also within the expected range compared to other *Cercocebus* spp. and other cercopithecines, with the exception of an earlier onset and longer duration of menstruation and implantation bleeding. Further information on the reproductive physiology of the Sanje mangabey is needed to clarify what factors are causing such unusual characteristics of these last two parameters in this species.

Keywords: adolescent, cycle length, fecal ovarian hormones, gestation, post-partum amenorrhea, Udzungwa Mountains

Introduction

A basic understanding of reproductive characteristics and ovarian endocrinology is necessary to address fundamental questions regarding the reproductive strategies and life history of a species (e.g., Harcourt, 1995; van Schaik and Janson, 2000). The reproductive characteristics of captive cercopithecine primates are relatively well known (Martin, 2007; Dixson, 2012); however, fewer data are available for wild species, as they are difficult and costly to collect, requiring recognition of individuals and long-term monitoring. As a result, most available information comes from captive populations, which tends to overestimate a species' reproductive rates due to the positive impact of a nutrient-rich diet on growth and reproduction (Ellison, 2003; Altmann and Alberts, 2005). For example, compared to their wild counterparts, in captive and provisioned populations females mature faster and have shorter gestation, shorter periods of post-partum amenorrhea (PPA) and shorter inter-birth intervals (e.g., Japanese macaques, *Macaca fuscata*: Takahata, 1980; Sugiyama and Ohsawa, 1982; Mori et al., 1997; Takahata et al., 1998; grey-cheecked mangabeys, *Lophocebus albigena*: Deputte, 1992; Guinea baboons, *Papio papio*: Gauthier, 1999; Hanuman langurs, *Semnopithecus entellus*: Borries et al., 2001; savannah baboons, *P. cynocephalus*: Altmann and Alberts, 2005).

In recent decades new data on reproductive characteristics of wild primate populations have become available (e.g., woolly monkeys, *Lagothrix lagotricha*: Nishimura, 2003; northern muriquis, *Brachyteles arachnoides hypoxanthus*: Strier et al., 2003; golden snub-nosed monkeys, *Rhinopithecus roxellana*: Qi et al., 2008; Assamese macaques, *M. assamensis*: Fürtbauer et al., 2010; Phayre's leaf monkeys, *Trachypithecus phayrei crepusculus*: Lu et al., 2010). Even so, a great disparity exists among genera, with some species, such as baboons and macaques, having received much attention in both captive and wild settings (Altmann and Altmann, 1970;

Lindburg, 1980; Altmann, 1998; Nakagawa et al., 2010; Swedell and Leigh, 2010), while others, such as mangabeys, particularly of the genus *Cercocebus*, are very poorly known (Ehardt and Butynski, 2006; McCabe and Fernández, 2011). Reproductive data from captivity are available for only two of the 4-6 *Cercocebus* spp. currently recognized (Field, 2003): the sooty mangabey (*C. atys*) and the golden-bellied (*C. agilis chrysogaster*) mangabey (Hadidian and Bernstein, 1979; Calle et al., 1990; Gordon et al., 1991; Whitten and Russell, 1996; Walker et al., 2004). Data from the wild are scarce and limited to two species, the Tana River (*C. galeritus*) and the sooty mangabey (Homewood, 1975; Kinnaird, 1990; Range et al., 2007).

Here we present the first data on ovarian endocrinology and reproductive characteristics of another species of wild *Cercocebus* mangabey, the Sanje mangabey, *C. sanjei*. We used non-invasive analysis of fecal estradiol (fE) and progesterone (fP) metabolites and behavioral observations to calculate reproductive parameters, including length of the menstrual cycle, number of cycles to conception, gestation length and duration of PPA; and to compare these parameters with other cercopithecine primates. We also report values for adolescents separate from those of adult females, as the reproductive characteristics of adolescent females are known to differ from those of parous females (Altmann et al., 1981; Dixson, 2012). In particular, adolescents can undergo a period of sterility during which they experience a series of irregular, anovulatory cycles (Hartman, 1931; reviewed in Dixson, 2012), leading to significantly longer menstrual cycles compared to those of adults (Hamadryas baboon, *P. hamadryas*: Bentley-Condit and Smith, 1997; chimpanzees, *Pan troglodytes schweinfurthii*: Wallis, 1997).

Due to the positive impact that food availability can have on reproductive parameters (Ellison, 2003; Altmann and Alberts, 2005), we expect wild Sanje mangabeys to have relatively slower reproduction rates (i.e., more cycles to conception, longer gestation and longer PPA) compared to captive mangabey populations. For example, provisioned populations of Hanuman langurs have been found to have shorter gestations than non-provisioned populations (Hanuman langurs: Borries et al., 2001), and captive grey-cheeked mangabeys have shorter PPA periods than wild populations (grey-cheecked mangabeys: Deputte, 1991). Furthermore, we expect Sanje mangabey reproductive rates to be comparable to those described for other wild mangabeys of similar body size (Harvey et al., 1987). In addition, as a result of the high energetic demands that lactation imposes on females (Lee, 1987), infant survival may have an impact on the reproductive rate. For example, in non-seasonally breeding species, females with a surviving infant need much longer to recoup the large amount of energy expended during lactation and thus, resume cycling again (van Schaik and van Noordwijk, 1985). In particular, females with a non-surviving infant undergo fewer cycles to conception than females with surviving infants (yellow baboons: Altmann et al., 1978). Similarly, females with surviving infants exhibit longer PPAs than females with non-surviving infants (yellow baboons: Altmann et al., 1977; sooty mangabeys: Hadidian and Bernstein, 1979; Hanuman langurs: Winkler et al., 1984; hamadryas baboons: Bentley-Condit and Smith, 1997; chimpanzees: Wallis, 1997; Japanese macaques: Takahashi, 2002). Female Sanje mangabeys live in a seasonal environment but are able to conceive and give birth throughout the year (Ehardt et al., 2005; McCabe, 2012); thus, we expect that females whose infants have died will undergo fewer cycles to conception and will have shorter PPA than females following a surviving offspring.

Methods

Study site and subjects

The study site is located within the Mwanihana Forest (7°40'–57'S, 36°46'–56'E) of the Udzungwa Mountains National Park, Tanzania. The habitat consists primarily of montane and sub-montane tropical forest comprised of deciduous primary and secondary growth (Lovett, 1993; Ehardt et al., 2005). The Udzungwa Mountains receive an average rainfall of 1,750 mm/year (Lovett, 1996), with the majority of rain (1,650 mm) occurring between November and May (McCabe, 2012).

Sanje mangabeys live in multi-male, multi-female groups (Ehardt et al., 2005). This research was conducted on the Mizimu group, habituated in 2004 (Ehardt et al., 2005). At the time of this study, the Mizimu group consisted of 63-65 individuals, including seven to ten adult males, 18 to 20 adult females, three adolescent females (see below), as well juveniles and infants. Births occurred throughout the year, although most were concentrated between July and September, while the majority of conceptions occurred between January and March (McCabe, 2012). During the menstrual cycle and in the first half of the gestation period, females develop an exaggerated sexual swelling of the perineal region (Ehardt et al., 2005; Chapter 3). Over the course of the study three females matured, and exhibited their first sexual swelling; thus, they were classified as adolescents. They were further characterized by a larger and brighter sexual swelling relative to those of adult females (Anderson and Bielert, 1994), button-like nipples (Altmann et al., 1977), smaller body size (Sigg et al., 1982) and less pigmented facial skin compared to adults. All adults and adolescents were individually identified using scars and facial coloration. Data presented here refer to 18 adult and three adolescent females.

Data collection

Data were collected in three consecutive periods: Period 1 (October 13th, 2008 - May 1st, 2009), Period 2 (June 11th, 2009 - July, 10th 2010) and Period 3 (August 21st, 2010 – September 27th, 2010). Data collection tasks were divided among myself and a team of five assistants: Clever P. Ngatwika (October 13th, 2008 - April 5th, 2010), Aly C. Mihambo (October 13th, 2008 - November 13, 2009), Bakari S. Ponda (March 14th, 2009 - September 27th, 2010), Francis J. Masinde (August 11th, 2009 - May 8th, 2010) and Aloyce M. Kigoma (April 11th, 2010 - July, 10th 2010). Whenever the group was contacted we followed it from dawn until dusk, except for two days in which we lost contact for 1.3 and 1.6 hours, respectively, due to the difficulty of the terrain which is comprised of steep hills and oversized rocks, and the group's large home range and daily path length (Ehardt et al., 2005).

During Period 1, the group was followed an average of 8.8 ± 4.3 days per month (range: 4 – 18, total = 70 days). This period was used to identify adult individuals and to train assistants. As adult individuals became individually recognizable (completed on December 1st, 2008), on each day the group was followed we (myself, CPN, ALC, FJM, AMK) attempted to record each female's sexual swelling size (Chapter 3) and presence of menstrual blood. We also recorded all infant births and deaths, sex of infants and incidence of nursing. In addition to the aforementioned data, during Period 2 we (myself, CPN, ALC, FJM, BSP, AMK) collected fecal samples for hormonal analysis (see Fecal Collection and Hormone Analysis below). Feces were also provided opportunistically by another research team working concurrently at the site (McCabe, 2012). In Period 2, we established a rotating schedule among the research team to ensure that every day the group was followed there were at least two people collecting data. Due to the difficulty of the terrain, however, the group could not be located for a total of 22 days (mean: 1.6 ± 2.2 days/month, range: 0 – 7 days/month). In addition, researchers were unable to complete a full day follow of the group on 35 separate days (mean: 5.8 ± 3.9 days/month). Overall, during Period 2 the group was followed an average of 23.1 ± 6.0 days per month (range: 10 – 30, total = 338 days), or 3,346.4 observation hours (10.36 ± 1.2 hours/observation day). We conducted inter-observer reliability tests every four months to ensure consistency in data collection among the different observers, requiring an agreement of at least 90% (Martin and Bateson, 2007). During Period 3, the group was followed every week for a total of five days to collect demographic data.

For calculations involving hormonal data and cycle length durations, we excluded data collected between March 27th and April 8th, 2010. At that time eight of nine cycling adults and one adolescent female began exhibiting significantly lower levels of fP, which was shortly followed by a significant increase in levels of fE, and an interruption in their regular swelling patterns (Fernández, unpublished).

Sexual swelling tumescence scoring

Sexual swelling tumescence was scored using a 9-point scale (Chapter 3). Each score on the scale indicated: 1) the absence of any sexual swelling (score 0); 2) a sexual swelling increasing in tumescence, i.e., inflation (score 1-4); 3) the period of maximum tumescence (score 5); and 4) a sexual swelling decreasing in tumescence, or the period of detumescence, i.e., deflation (score 6-8). At some point during maximum tumescence, the appearance of the sexual skin usually changed, acquiring a darker and shinier tone, as if covered with a thin, oil film (Chapter 3), which was noted. The scale was designed to capture relative, rather than absolute changes in the tumescence of the swelling. Two females, therefore, may have the same swelling score (e.g., score 5) but one of them may display a swelling that is of absolute larger size.

Reproductive data

During data collection, we used changes in the tumescence of the sexual swelling, as well as nipple contact with an infant, to classify females into three reproductive states: cycling, pregnant, and in PPA. Females were defined as cycling when they underwent successive cycles of sexual swelling inflation and deflation, reaching maximum, or near maximum tumescence at approximately 30 day intervals (Hadidian and Bernstein, 1979; Whitten and Russell, 1996; Walker et al., 2004; Chapter 3). Pregnant females were identified by the development of a post-conceptive sexual swelling which reached maximum tumescence approximately 50 days after the end of the period of maximum tumescence of the conceptive cycle (Hadidian and Bernstein, 1979; Kinnaird, 1990; Gust, 1994; Walker et al., 2004; Chapter 3). Conceptions were ultimately confirmed hormonally when such data were available (see below) and/or with the birth of an infant approximately 173 days after the conceptive cycle (Stabenfeldt and Hendrickx, 1973; Kinnaird, 1990). After the birth of an infant and until a female's sexual swelling began inflating again, females were categorized as in PPA.

A total of 24 infants were born during the study, 10 during Period 1, eight during Period 2, and six during Period 3. Date of birth for infants born during non-observation days (N = 3 for Period 1; N = 8 for Period 2) was estimated as the middle day between the last day a female was observed without an infant and the day the infant was detected, unless otherwise indicated. At the beginning of the study, five infants were present and their age was estimated to be six weeks based on precociousness and pelage color. An infant that disappeared was presumed dead (N = 10 infants).

Fecal sample collection and hormone analysis

Fecal samples were collected on 311 days during Period 2. In total, we analyzed 936 samples, including 735 from adult females (84 of which were from pregnant females) and 201 from adolescent females (Table 2.1). Due to impaired visibility, the high number of females in the group and shortage of trained observers, we prioritized data collection for females to the period near or during maximum tumescence to ensure the detection of ovulation. On average, cycling females were sampled every 1.9 ± 0.9 days (range: 1-5 days) when they were approaching or were in maximum tumescence, and every 4.5 ± 2.1 days (range: 1-12 days) outside this period. Pregnant females were sampled every 4.6 ± 2.5 days (range: 1 – 19 days). The sampling frequency for adolescent females was every 2.3 ± 1.0 (range: 1-8) for those approaching or in maximum tumescence, and 5.2 ± 3.1 days (range: 1-20) outside this period.

Fecal collection and processing were modified after Brockman and Whitten (1996). Entire, freshly deposited samples that had not been in contact with urine were placed in a Ziploc® bag with a small silica gel package to initiate drying and placed inside a thermos with an ice pack that had been cooled overnight in a mountain stream. Within two to eight hours, samples were packaged in aluminum foil, flattened and labeled. Once extraneous items such as seeds or dirt were removed using a stick, samples were dried in a Coleman® oven at 55-83 °C for two to three hours or until dry. Dried samples were stored in labeled Ziploc® bags with silica gel to absorb moisture at ambient temperature until shipped to the Smithsonian's National Zoological Park, Front Royal, VA, in August 2010 for analysis. The methods of collection and preservation were validated at Dr. Patricia Whitten's Reproductive Ecology Laboratory, Emory University, using feces from related *C. atys* housed at the Yerkes National Primate Research Center. More specifically, the analysis of 15 fecal samples collected during one cycle indicated lower levels of ovarian hormones in dried compared to frozen samples; the profiles, however, were nearly identical. Similarly, peak hormone levels were comparable to levels observed in other mangabey studies (Whitten, pers. comm.).

Fecal extraction was conducted by J.L.B. as previously described in Velloso et al. (1998). In brief, samples were freeze-dried, crushed, sifted to get rid of extraneous material and put into storage tubes until analysis. Crushed fecal samples were weighed in 16 x 125 mm glass tubes (~0.2 g each), and extracted with 5ml of 90% ethanol along with 100µl tritiated progesterone tracer to monitor extraction efficiency. Samples were then capped with rubber stoppers and placed on a multi-pulse vortex for 30 minutes. Samples were centrifuged at 1,500 *g* for 15 minutes. The supernatant was transferred to a new set of 16 x 125 mm tubes. The fecal pellet was then re-suspended in 5ml of 90% ethanol, vortexed for 30 seconds and centrifuged at 1,500 *g* (15 minutes). The new supernatant was combined with the previously decanted one and dried under air. Immediately prior to extraction, the extractant was reconstituted in 1ml of dilution buffer (0.1M $NaPO_4$, 0.149M NaCl, pH 7.0), vortexed and placed, covered, in an ultrasonic glass cleaner for 15 minutes or until extractant was completely in solution. Average fecal extraction efficiency was 76.4 ± 15.2%.

Extracted samples were diluted in buffer 1:20 – 1:60 for estrogen, and 1:100 – 1:400 for progesterone analyses. Fecal estradiol and fP metabolites were quantified using enzyme immunoassay (EIA) procedures. The estradiol antiserum (R4972; Coralie Munro, UC California, Davis, CA) was raised in rabbits and had cross-reactivities of 100% with estradiol, 3.3% with estrone, 0.8% with progesterone, 1.0% with testosterone and androstenedione, and <1% with cortisol and dihydrotestosterone (C. Munro, pers. comm.). The fP assay relied on a monoclonal progesterone antibody (CL425; C. Munro), which cross-reacts 100% with progesterone, 96%

with 5α-pregnane-3β-ol-20-one, 36% with 5α-pregnane-3β-ol-20-one, 36% with 5α-pregnane-3α-ol-20-one, 15% with 5β-pregnane-3bo1one, 15% with 17β -hydroxyprogesterone, 13% with pregnenolone, 7% with 5 β -pregnane-3α-ol-20-one, 5% with 5 β-pregnane-3α-ol-17α-diol, one, and < 1% with pregnanediol-3-glucuronide, androstenedione, testosterone, estradiol, estrone, estriol, 21-hydroxyprogesterone, 20α-hydroxyprogesterone, and cortisol (Grieger and Scarborough, 1990; Wasser et al., 1994). Inter-assay CVs (N = 32) for the fE assays were 8.3% for low and 8.8% for high controls. For the progesterone analysis, inter-assay CVs (N = 39) were 5.5% and 10.5% for low and high controls, respectively. Assay sensitivities were 40 pg/ml and 50 pg/ml for the estradiol and progesterone assays, respectively. Recovery of exogenous steroid added to pooled samples before extraction averaged 93.3 ± 8.1% (N= 2/hormone). All hormone values are expressed in nanograms of hormone per milligram of dry feces.

Menstrual cycle parameters

In primates, menstrual cycle parameters are commonly defined based on fluctuations in estrogen (e.g., Yan and Jiang, 2006), progesterone (e.g., Heistermann et al., 2001b; Deschner et al., 2003; Engelhardt et al., 2005; Barelli et al., 2007), both (e.g., Whitten and Russell, 1996; Higham et al., 2008b; Lu et al., 2010), or a combination of hormonal data and other physical markers such as the presence of menstrual blood or changes in sexual swelling tumescence (e.g., Emery and Whitten, 2003). To date, only two studies, both conducted in captive populations, have examined the endocrinology of the menstrual cycle of a *Cercocebus* mangabey, (white-crowned mangabey [*C. atys lunulatus*]: Aidara et al., 1981; sooty mangabey: Whitten and Russell, 1996). Whitten and Russell (1996) used estrogen fluctuations to determine cycle length (i.e., days between estrogen peaks), and both estrogen and progesterone to mark the beginning of the luteal phase, defined as the onset of the estrogen decline after its ovulatory peak that is followed by a progesterone rise. Here we will calculate cycle length from the first day of menses to the last day before the next menses. Fecal progesterone and fE showed relatively large fluctuations during the luteal phase (Figure 2.1), which combined with a low sampling frequency outside the period of maximum tumescence, precluded us from using it to calculate menstrual cycle parameters. Furthermore, because in this species menstrual blood appeared consistently much earlier (see Results) than what has been reported for the related *C. atys* and for other cercopithecines, we could not use menses to mark the beginning of the follicular phase.

Detection of Ovulation

To approximate the time of ovulation, we aimed to identify the estrogen surge that occurs prior to ovulation (Saltzman et al., 2010). To do so, for each cycling female we first calculated a baseline value of fE using an iterative process following Brown et al. (1996) by which all values exceeding 1.5*SD above the mean were excluded. The fE baseline was then calculated by averaging the remaining values (Brown et al., 1996). Next, we calculated the fE surge threshold, defined as 1.5 times above the aforementioned baseline (Brown et al., 1996). The baseline was calculated for each female individually; therefore, the threshold that defined an estrogen surge differed among females. Finally, we identified all fE peaks, that is, all fE values exceeding the threshold. In addition, because of fluctuations in baseline fE, only those fE peaks that rose above the ovulatory threshold and that were clearly higher than other fE values for that cycle, were identified as estrogen surges (Figure 2.2). In cases when there were other fE values lower but relatively similar to the highest fE value, they were also considered part of the fE surge. A similar method was applied to fP with the aim of detecting the post-ovulatory progesteron rise that would confirm that ovulation occurred. Fecal progesterone values, however, were highly variable and remained elevated throughout the menstrual cycle (Figure 2.1), yielding it uninformative in regards to confirming ovulation. Thus, in this study we used a significant surge of fE alone as a proxy for ovulation.

Since ovulation typically occurs during maximum swelling in the related sooty mangabey (Aidara et al., 1981; Whitten and Russell, 1996), as well as in many other cercopithecines (e.g., Wildt et al., 1977; Engelhardt et al., 2005; Möhle et al., 2005; Higham et al., 2008a; Daspre et al., 2009), we restricted the analyses of ovulation to those cycles (adults: N = 9; adolescents: N = 3 cycles) with hormonal sampling on at least 50% of the days of maximum tumescence (average length: 7.1 ± 2.1 days; Chapter 3) to ensure the detection of the estrogen surge. When no hormonal samples were available from the day immediately before and/or after the fE peak, we could not rule out the possibility that the peak occurred on these days. We, therefore, defined an ‘ovulatory window’ rather than a single day of estrogen surge, which included the day(s) fE rose above the fE surge threshold and was clearly higher than other fE values, plus the day(s) without samples on either side of it. We constructed a composite profile for adult females that included five non-conceptive cycles in which we identified the fE surge. Cycles were aligned to the day of highest fE value (Figure 2.3).

To calculate the average fE and fP during the menstrual cycle we used cases in which we had two consecutive cycles in the same female in which we were able to detect the fE surge (N= 2 adult cycles). To do so, we averaged all fE and fP samples from the start of the ovulatory window to the last sample before the ovulation window of the following cycle. None of the cycles of adolescent females in which we detected the fE surge were consecutive, thus we could not calculate average fE and fP levels for the adolescents’ menstrual cycle.

In a closely related species (*C. atys)*, it takes between 0 and 2 days for serum estradiol to be metabolized and to appear in feces (Whitten and Russell, 1996). We used the mid-point; i.e., 24 hours, as the average time lag to account for this metabolism (Whitten, pers. comm). Typically, ovulation occurs an average of 24 hours *after* estrogen peaks in the blood (Jeffcoate, 1983); therefore, we assigned the day of estrogen surge as the day fE exceeded the baseline in the feces (Higham et al., 2008b).

Conception, gestation and post-partum amenorrhea

The conceptive swelling was defined as the last swelling occurring before the post-conceptive swelling. Conceptions were further identified hormonally in three cases, during which fE levels remained elevated after the ovulatory peak. To calculate gestation length, we only included those cycles in which we observed the conceptive swelling and we could confidently assign the date of birth (N = 8 gestations). In cases when ovulation was not detected (N = 5), we assigned the day of conception as the last day of maximum tumescence, because in the three conceptive cycles in which ovulation was detected it occurred towards the end of maximum tumescence (Chapter 3). This is supported by a study of baboons using laparoscopy to detect ovulation which found that in 89% of cycles detumescence started within 3 days of ovulation (Shaikh et al., 1982). Once the day(s) of conception and the date of birth were determined, we calculated the maximum and minimum possible gestation length and averaged both values. We created a fE composite profile using hormonal data for two complete gestations, averaging weekly fE values aligned from the week of birth.

Post-partum amenorrhea was defined as the number of days from the date of parturition to the day before the start of the next sexual swelling (Altmann et al., 1977). Only females with a surviving infant were included. For females with non-surviving infants, we calculated the number of days from the infant’s disappearance to the first day with a swelling (N = 6). When the first day of the start of a swelling was not known (N = 3), it was estimated by calculating the mid-point between the last observation day when the female had no swelling and the first day with a swelling.

Data treatment

For the calculation of the characteristics of the menstrual cycle parameters and the duration of PPA after a death infant, we limited our calculations to instances in which we knew the exact start and end day of each parameter. To avoid underestimating durations we also examined all cases that could be determined to within 1 or 2 days. We report these values only when they fall outside the range of variation observed in the more precise data set. Prior to analysis, we screened data for equal variance, normal distribution and outliers. Outliers were identified using the 'Outlier' function in SPSS® and were defined as values whose distance from the nearest quartile is greater than 1.5 times the interquartile range. As our sample size was small, we used each measure (e.g., cycle length), rather than each female, as the unit of analysis. Differences in fE and fP during the menstrual cycle, conception, gestation and PPA, and between adult and adolescent females were assessed using a Mann-Whitney U test. All statistical analyses were performed in SPSS® 19.0 for Mac. All tests were two-tailed and evaluated with an alpha level of 0.05.

Results

Results of hormone assays

In total, we identified nine cycles of adult females that were sampled on at least 50% of the days during and around maximum tumescence, including five non-conceptive, one conceptive and one anovulatory cycle (Table 2.2). In five cases, there were several samples above the fE surge threshold. In four of those cases, there was a sample clearly above the rest

(Figures 2.4, 2.5, 2.6, 2.7). In the fifth case, none of the three samples above the baseline were clearly higher and all of them were considered part of the ovulatory window (Figure 2.8). In three other cases, only one sample rose above the fE baseline. In two of these, the fE peak was clearly higher than other values (Figures 2.9, 2.10), while in the third case the fE value was similar to the sample collected the day immediately after, and thus both days were considered potential days of ovulation (Figure 2.11). Finally, in one cycle that was sampled daily from three days before maximum tumescence to one day after, none of the values rose above the ovulatory threshold and thus that cycle was considered anovulatory (Figure 2.12). For adolescent females, only three cycles were sampled 50% of the days during and around maximum tumescence (Table 2.2). In each of these cycles, we could identify one sample with fE above the baseline that was clearly higher than other values (Figure 2.13, 2.14, 2.15).

Menstrual cycle

Menstruation was visible in 84.0% of the cycles of adult females for which the female was observed during detumescence (42 of 50 cycles), beginning on average 5.7 ± 2.8 days (range: 1 – 11; N= 12 cycles) after the onset of detumescence (i.e., after the last day of maximum tumescence; Table 2.3), and lasting an average of 6.6 ± 2.6 days (range = 2 – 10 days, N = 9 cycles). Menstrual blood, however, was not always visible every day. The extended data set (i.e., when values were known to within 1 - 2 days) indicated a range of menses duration from 1-12 days (Table 2.3). Cycle length, calculated from the first day of menses to the day before the next menses, averaged 30.0 ± 3.0 days (range: 27-33; N= 3) (Table 2.3).

Adolescent females exhibited menses in 88.8 % (16 of 18) of cycles for which there were data during detumescence (Table 2.3). Adolescent menses began an average of 4.8 ± 0.5 days (range: 4-5; N= 4; range = 4-8 when extended data set is included) following the onset of detumescence, and lasted an average of 9.2 ± 5.6 days (range: 3-16; N= 5; range = 22-20 extended data set, n = 7; Table 2). As in adults, once menses began, it was not always visible every day. Cycle length calculated using menses averaged 49.0 ± 6.3 days (range: 41-56; N= 3; extended range = 41-58, n = 4) which was significantly longer than the average cycle length in adult females calculated using menses (Mann-Whitney U: z = 2.323, p = 0.024).

Fecal estradiol averaged 392.9 ± 88.9 ng/mg (range: 247.0 – 540.5; N = 2 cycles) during the menstrual cycle, while fP averaged 719.1 ± 419.5 ng/mg (247.0- 1,946.9; N = 2 cycles). Fecal estradiol levels of adult female ovulatory cycles reached an average of 497.8 ± 92.3 ng/mg during maximum tumescence (range: 368.6 – 673.0; N = 8 cycles), and peaked at an average of 683.2 ± 141.0 ng/mg (529.0 – 910.0; N = 8 cycles) during the fE surge (Table 2.2). The single anovulatory cycle displayed an average fE of 488.1 ± 61.5 ng/mg during maximum tumescence, with a maximum fE value of 575.8 ng/mg (Table 2.2). Fecal progesterone during the menstrual cycle of adult female averaged 719.1 ± 419.5 ng/mg (range: 247.0 – 1,946.9; N = 2 cycles), reaching an average of 1,679.5 ± 476.6 ng/mg (range: 888.3 – 2,302.9; N = 8 cycles) during the ovulatory window defined using the fE surge. On occasion, however, fP levels peaked higher during the follicular phase, before the fE surge, as revealed by the composite profile of non-conceptive ovulatory cycles (Figure 2.3).

Average hormonal levels during the menstrual cycle of adolescent females could not be calculated because none of the cycles in which the fE surge was detected were consecutive. During maximum tumescence, fE in adolescent females averaged 514.7 ± 99.3 ng/mg (range: 445.6-628.5; N = 3 cycles), which was not significantly different compared to adults (Mann-Whitney U: z = 0.000, p = 1.000). During the fE surge, fE levels increased to an average of 706.0 ± 71.7 ng/mg (range: 628.4-769.7; N = 3 cycles), which did not differ from adult levels

(Mann-Whitney U: *z* = 0.204, p = 0.838). Fecal progesterone levels of adolescents during the ovulatory window averaged 1,668.7 ± 575.6 ng/mg (range: 1,139.8-2281.7; N = 3 cycles), which was also not significantly different than fP surges during the ovulatory window in adults (Mann-Whitney U: z = 0.000, p = 1.000).

Conception, gestation and post-partum amenorrhea

Adult females took fewer cycles to conceive following the death of an infant (mean = 2.5 ± 1.3 cycles, range: 1 – 5; N = 8 conceptions) compared to when mating resumed after a surviving offspring (mean = 4.3 ± 1.5 cycles, range: 3 – 6, N = 4 conceptions), a difference that approached significance (Mann-Whitney U: *z* = 1.860, p = 0.073). Following conception, bleeding was observed in all cases (N = 8). It began on average 17.5 ± 0.7 days (range: 17-18 days, N= 2 conceptions) after the end of maximum tumescence, and lasted for an average of 10.0 ± 1.4 days (9-11 days; N= 2 cases; Table 2.3). The range of variation, however, is greater when the expanded data set is considered, with bleeding onset as early as 3 - 4 days after the end of maximum tumescence. The number of days after the ovulatory fE peak to the start of implantation bleeding could not be determined. Adolescent females failed to conceive throughout the study period despite cycling for up to 16 months.

Analysis of the three conceptive cycles for which a fE surge was detected revealed that in the first week of gestation, fE dropped to an average of 445.6 ± 17.4 ng/mg, but rose again immediately after. Average fE values during the first two weeks of gestation (492.0 ± 71.5 ng/mg; range: 433.0 – 604.4; N = 5 days) were significantly higher than average fE values three weeks prior to conception (374.1 ± 86.1 ng/mg; range: 266.4 – 541.0; N = 15 days; Mann-Whitney U: *z* = 2.313, p = 0.019). Fecal progesterone after the fE surge during conceptive cycles averaged 1027.0 ± 228.9 (741.9 – 1,338.4; N = 5 days), slightly lower compared to the three weeks prior to conception (average: 1,293.0 ± 457.8 (544.0 – 1,982.9; N = 15 days). This difference was not significant (Mann-Whitney U: z = -1.440, p = 0.168).

Mean gestation period was 171.8 ± 3.4 days (range: 168.0-178.5; N = 8 pregnancies). Fecal estrogen increased steadily throughout gestation (Figure 2.16) from an average of 504.0 ± 200.3 ng/mg (range: 197.5-991.6; N = 12 weeks) during the first trimester to an average of 823.9 ± 363.9 ng/mg (range: 502.7-1933.0; N = 13 weeks) during the second trimester, a difference that was significant (Mann-Whitney U: z = 3.406, p = 0.002). Two weeks before birth fE underwent a further surge, reaching a mean of 1441.8 ± 695.9 ng/mg (949.7 – 1,933.9 ng/mg), which was significantly higher than average fE values during the remainder of the gestation period (N = 22 weeks; Mann-Whitney U: z = 2.170, $p < 0.017$). Fecal progesterone also increased during gestation, from an average of 2,003.3 ± 857.5 ng/mg (range: 1,296.8 – 3,791.0; N = 12 weeks) in the first trimester to an average of 2,772 ± 938.1 (1,146 – 4608.4; N = 13 weeks) in the second trimester, an increase that was statistically significant (Mann-Whitney U: z = 2.013, p = 0.046). For a period of six weeks, from week 15 to 10 prior to birth, fP surged, reaching an average of 3,502.3 ± 716.6 ng/mg (2,423.5 – 4608.4; N = 6 weeks), which was significantly different than average fP outside this period (Mann-Whitney U: z = -3.054, p = 0.001). Females with surviving infants first developed a sexual swelling an average of 6.7 ± 2.3 months post-partum (range: 3.8 - 13.3 months; N= 15 cases). After the death of an infant, females quickly resumed cycling with sexual swellings developing an average of 14.3 ± 5.9 days, and as rapidly as 8 days, following infant death (range: 8 – 23 days; N = 6 cases).

Discussion

In this study, we used non-invasive analysis of ovarian hormones and group follows to provide the first data on the reproductive endocrinology and characteristics of a wild *Cercocebus* mangabey, and the first such data for the Sanje mangabey. This study found that the composite profile of Sanje mangabey fE levels resembled profiles reported for sooty mangabeys in which fecal and serum estradiol were analyzed (Aidara et al., 1981; Whitten and Russell, 1996). Given that the only study that measured fecal metabolites used radioimmunoassay procedures (Whitten and Russell, 1996), rather than enzyme immunoassays as used here, concentrations of fE for sooty and Sanje mangabeys are not comparable. Similar to sooty mangabeys (Whitten and Russell, 1996), Sanje mangabeys showed a clear fE rise starting at day -2 leading towards the fE surge and declining steeply immediately after. This also supports what Gust (1994) found in sooty mangabeys, in which estradiol showed an acute rise around the time of ovulation which may be difficult to capture unless sampled daily. Sanje mangabey did not show, however, the sustained increase prior to this rise, although this is probably due to the lower sampling frequency at this time. Also, as expected, fE peaked during the maximum tumescence period. In one of the individual profiles for an adolescent female (Figure 2.15), there was another, lower, fE peak 11 days after the fE surge. This peak, however, was associated with the onset of menstruation, when estradiol levels tend to increase slightly again (Jeffcoate, 1983; Saltzman et al., 2010).

Fecal progesterone, on the other hand, showed virtually no similarities to the composite profile of sooty mangabeys. Rather than being at low levels during the follicular phase until the luteinization of the granulosa cells, when it should have started increasing as the corpus luteum developed (Saltzman et al., 2010), fP remained relatively high and fluctuating, reaching its highest levels the day before the fE surge. Similarly, after the fE surge, rather than remaining elevated, fP showed a steep decline. The causes of this are not clear. It might have been caused by preservation and/or storage conditions (Khan et al., 2002; Washburn and Millspaugh, 2002; Lynch et al., 2003), the diet of the animals (Wasser et al., 1993) or it may the excreted progesterone metabolite in this species that was not recognized by the antibody. As a consequence, in this study we had to use the estradiol surge that precedes ovulation (Saltzman et al., 2010) as a proxy for ovulation. Analysis of fP would have been required to confirm that ovulation occurred. We are, however, confident that the fE surge is a valid proxy for ovulation because a temporal and quantitative relationship between fecal and serum estradiol, and between serum estradiol and the peri-ovulatory peak of FSH has previously been documented in mangabeys. In particular, in *C. atys,* fE levels significantly correlated with levels of serum estradiol, with fE peaks lagging 0-2 days behind serum peaks (Whitten and Russell, 1996), and serum estradiol correlated with FSH (Aidara et al., 1981).

One of the cycles for which we have hormonal data very likely was anovulatory. However, in this study, sampling frequency for females outside the maximum tumescence period was less than half that of sampling frequency during maximum tumescence which might bias baseline values toward higher values because estradiol is higher during and around maximum tumescence. This would make it less likely that a given fE value was higher than the baseline, and thus might have caused us to wrongly classify a cycle as anovulatory (i.e., not showing the estradiol surge) if the peak in fE was relatively low. The cycle that was classified as anovulatory was sampled on a daily basis during and around maximum tumescence. It exhibited a steady and slow rise but it lacked a clear peak in fE compared to the other cycles, which would have indicated the estrogen surged (Figure 2.12). In addition, all samples in this cycle demonstrated very low fE values during and around the period of maximum tumescence. Thus, we are confident in our classification of this cycle as anovulatory and that it is not an artifact of the sampling frequency.

Adult and adolescent females showed similar values of fE during maximum tumescence and during the fE surge. The levels of fP during the ovulatory window are also comparable. Adolescents, however, exhibited significantly longer menstrual cycles than adults, and cycled for up to 16 consecutive months without conceiving, which demonstrates that adolescent Sanje mangabeys undergo a period of adolescent sterility (Hartman, 1931). In a study of captive female rhesus monkeys, although most adolescent menstrual cycles were anovulatory, occasionally they would undergo ovulatory cycles (Bercovitch and Goy, 1990). This may explain why adolescent Sanje mangabeys failed to conceive, as well as why we detected three cycles with a fE surge during this period of sterility.

The reproductive parameters of Sanje mangabeys fell within the ranges of those reported for other mangabeys. For example, adult female menstrual cycle length averaged 30.1 days, comparable to the mean of 29.4 ± 1.6 days based on sexual swelling data (Chapter 3). These values are very similar to those reported for captive golden-bellied mangabeys (31.0 ± 1.6 days, Walker et al., 2004) and captive sooty mangabeys (30.1 ± 4.0 - 31.8 ± 0.4 days, Gordon et al., 1991; Whitten and Russell, 1996). Sanje mangabeys also displayed comparable cycle lengths compared to other cercopithecines, such as black mangabeys (*L. aterrimus*: 31.3 ± 5.0 days, Calle et al., 1990), and Asian macaques: 28.0 ± 3.4 in captive bonnet macaques (*M. radiata*: Rao et al., 1998), 30.1 ± 7.0 in wild Assamese macaques (*M. assamensis*: Fürtbauer et al., 2010), and 32.2 ± 3.0 in captive lion-tailed macaques (*M. silenus*: Heistermann et al., 2001a). The Sanje mangabey falls within the lower range of variation compared to the closely related *Mandrillus* sp. that in captivity had an average cycle length of 33.5 and 35.0 days (*M. sphinx*: Hadidian and Bernstein, 1979), as well as compared with wild *Papio spp.*: *ca.* 42 days in olive baboons (*P. anubis*: Higham et al., 2009) and 37.2 days in yellow baboons (Bentley-Condit and Smith, 1997).

With a surviving infant, females took, on average, almost twice as long to conceive again compared to when they had lost their previous infant (4.3 vs. 2.5 cycles). These values are similar to what has been described for captive sooty mangabeys after a surviving infant (median: 3.0 cycles, range: 1-7, Hadidian and Bernstein, 1979), and within the range of what has been described for non-seasonal cercopithecines such as captive olive baboons (3.6 cycles after a surviving infant, Garcia et al., 2006) and captive hamadryas baboons(2.2 and 3.5 cycles [range: 1-8 cycles], infant survival not specified, Sigg et al., 1982; Kaumanns et al., 1989), as well as for wild hamadryas baboons (4.1 cycles, infant survival not specified, Bentley-Condit and Smith, 1997) and semi-free ranging mandrills (range 1-8, 87% on first cycle; range: 1 – 8 cycles, infant survival not specified, Setchell and Wickings, 2004). The difference between females with surviving and non-surviving infants may be due to the fact that after an infant dies, the inhibitory effect that the suckling stimulus has on the release of the hypothalamic gonadotropin-releasing hormone, and consequently on the menstrual cycle (reviewed in Saltzman et al., 2010), disappears abruptly, allowing females to resume regular menstrual cycling. In contrast, in females with surviving offspring, which in Sanje mangabeys continue nursing well into gestation (Fernández, unpublished) the inhibitory effect of suckling decreases slowly. This may not impede the resumption of menstrual cycling but might inhibit ovulation, thereby increasing the number of cycles to conception. In addition, differences in stored energy levels between females with and without a surviving offspring may also play a role in the difference in number of cycles to conception, as lactation is the most energetically demanding period of the reproductive cycle

(Lee, 1987). In Sanje mangabeys, energy balance (i.e., energy intake minus expenditure, Emery Thompson and Wrangham, 2008) positively correlates with fecal estradiol, which increases as the female undergoes consecutive menstrual cycles (McCabe, 2012; McCabe et al., in review). Females whose infant had died would not have expended as much energy as females with a surviving infant; thus, such females might be able to recoup faster and produce the required estradiol levels earlier to ensure ovulation and conception (Strier and Ziegler, 2005), compared to those females who still had a dependent infant.

The gestation length of the Sanje mangabey was determined to be *ca.*172 days, within the range reported for captive *Cercocebus spp.,* with a mean of *ca.* 167 days in sooty mangabeys (Hadidian and Bernstein, 1979; Gordon et al., 1991) to *ca.* 179 days in the golden-bellied mangabey (Field, 2003; Walker et al., 2004). The only other wild mangabey for which there is information available, the Tana River mangabey, had a mean gestation length of 180.0 ± 4.5 days (Kinnaird, 1990). No data are available on the body size of Sanje mangabeys, but if we assume its weight to be similar to the closely related Tana River mangabey (Females: 5,260 kg; Fleagle, 1999), then our results indicate that Sanje mangabeys have a gestation length comparable to the similar-sized grey-cheeked mangabey, which in captivity has a mean gestation length of 174.7 ± 2.5 days (Kinnaird, 1990); but longer than the average gestation reported for wild macaques of similar body size (Fleagle, 1999), such as Assamese macaques (164.2 ± 4.0 days: Fürtbauer et al., 2010), and pig-tailed macaques (*M. nemestrina*: 163.0 ± 3.1 days, Melnick and Pearl, 1987); as well as to those of slightly smaller body size (Fleagle, 1999): *ca.*163 days in Formosan macaques (*M. cyclopis*: Hsu et al., 2001), and 163.0 ± 3.1 days in crab-eating macaques (*M. fascicularis*: Engelhardt et al., 2006). Compared to wild baboons, which have a larger body size (Fleagle, 1999), the Sanje mangabey has a shorter gestation length: 185-192 days in olive baboons (Higham et al., 2009), and 181.5 days in yellow baboons (Bentley-Condit and Smith, 1997).

Post-partum amenorrhea after a surviving infant averaged 6.7 months, but it was highly variable across females, with a difference that was more than four-fold between the shortest and longest observed PPA (3.3 vs. 13.3 months). Dominance rank might have an effect on Sanje mangabey PPA, as females have dominance relationships with clearly high and low ranked individuals (McCabe, 2012; Fernández, unpublished). As energy balance influences estradiol levels (McCabe, 2012), and estradiol levels must reach a minimum threshold in order for menstrual cycling to resume (Strier and Ziegler, 2005), it is possible that if rank determines access to quality food resources, dominance rank might also influence the duration of PPA. For example, in chimpanzees, high-ranking females had higher infant survival, faster infant growth rates and earlier maturation of daughters, which the authors attributed to access to better foraging areas by dominant females compared to subordinates (Pusey et al., 1997). Similarly, seasonality of food availability might also influence the duration of PPA. In particular, females with surviving infants may have to wait until food availability increases in order to be able to improve their physical condition and start cycling again (van Schaik and van Noordwijk, 1985). In the study group's home range, food availability began increasing in September and peaked in March, when most conceptions occurred (McCabe, 2012), and there is evidence that most females resumed cycling between January and March (Fernández, unpublished). Thus, as food availability increased, females with surviving offspring may have finally been able to replenish the energy spent during lactation in order to resume cycling again. How much of an effect female rank and seasonality have on food intake and ultimately on PPA, however, remains to be investigated.

One surprising finding in our study was that menstruation began rapidly following detumescence. In Sanje mangabeys ovulation typically occurs during maximum swelling and usually within 3-4 days from detumescence (Chapter 3). Here we observed, however, that the onset of menstrual bleeding in adult females began an average of six days following the onset of detumescence. The duration of menses was also longer in Sanje mangabeys (*ca.*7 days in adults, *ca.* 9 days in adolescents) compared to other primates (reviewed in Hrdy and Whitten, 1987; golden-bellied mangabeys: 3.0 ± 0.4 days; range 1-6, Walker et al., 2004). The beginning of menses is triggered by the drop in progesterone that occurs when the ovum is not fertilized (Saltzman et al., 2010), and marks the end of the luteal phase and the beginning of the subsequent follicular phase. This would yield a luteal phase (i.e., time from ovulation to beginning of follicular phase) of approximately 6-9 days, considerably shorter than all previously published values for cercopithecines (Saltzman et al., 2010; Dixson, 2012), such as the sooty mangabey (15.7 ± 1.0 days, Gordon et al., 1991), the golden-bellied mangabey (13.4 ± 1.2 days, Walker et al., 2004) and chacma baboons (*P. ursinus*: 14.4 ± 2.2 days, Bielert and Girolami, 1986). This is highly unlikely as the luteal phase is a rather conserved value in catarrhine primates (Nelson, 2005). It is possible then, that progesterone drops earlier in Sanje mangabeys than in other species, such as *C. atys,* where it drops *ca.* 11 days after ovulation (Aidara et al., 1981; Whitten and Russell, 1996). This would explain the early occurrence of menses and its long duration. Accordingly, if we calculate the number of days from the start of detumescence to the end of menses (average = 12.7 ± 4.0 days [range: 7-19, N = 12] for adult females; 14.6 ± 4.9 days [range: 8-20; N = 5] for adolescent females), we obtain a value more similar to the luteal phases of other species. Alternatively, it could be argued that the pattern of menses observed in *C. sanjei* was an artifact of inadequate sampling or hormonal irregularities of the females.

However, this is also unlikely, as cycle length calcrulated from the beginning of one menses to the next is very similar to cycle length calculated using maximum tumescence (Chapter 3). Those values would have differed if menses had been a poduct of flawed sampling. Instead, it suggests that in *C. sanjei*, menses begins unusually early and therefore, might not be an adequate marker of the end of the luteal phase.

Similar to the pattern found for menstruation, implantation bleeding also occurred earlier (~18 days from detumescence) in this species than in others (sooty mangabeys: 24.8 ± 1.1 days, Gordon et al., 1991; golden-bellied mangabeys: 33 days, Walker et al., 2004), and for longer (~11 days) (Barbary macaques, *M. sylvanus*: 1-7 days, Küster and Paul, 1984; sooty mangabeys: 8.2 ± 0.5 days, Gordon et al., 1991). Further information on the reproductive physiology of the Sanje mangabey is needed to clarify what factors are actually causing the early appearance and long duration of menses and implantation bleeding in this species.

In summary, we have provided the first data on the reproductive characteristics and physiology of wild Sanje mangabeys. Adult females exhibited comparable fE levels during the menstrual cycle to other mangabeys, as well as reproductive characteristics within the expected rate range compared to other cercopithecines, with the exception of the early onset and long duration of menses and implantation bleeding. In addition, we demonstrated that adolescent Sanje mangabeys undergo a period of adolescent sterility, as has been described for other taxa. This study, therefore, provides the necessary information to examine fundamental questions regarding the reproductive strategies and the viability of the remaining population of this Endangered primate.

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Figures and tables

Table 2.1. Sampling periods and fecal samples collected per female. Females are alphabetized within each age class. Each female's sampling period represents a separate reproductive state.

Age class	Female ID	Period sampled	N samples collected	Reproductive state
Adult	bad[1]	06/14/09-12/13/09	43	Cycling
Adult	bad	06/13/10-07/08/10	10	Cycling
Adult	ham	02/09/10-07/09/10	31	Cycling
Adult	kab	03/05/10-06/30/10	21	Cycling
Adult	kim	02/09/10-06/26/10	35	Cycling
Adult	ksk	01/14/10-04/11/10	21	Cycling
Adult	ksr	07/11/09-01/30/10	69	Cycling
Adult	ksr	05/03/10-06/15/10	8	Pregnant
Adult	ksr	06/20/10-07/10/10	11	Cycling
Adult	kum	06/16/09-03/05/10	61	Cycling
Adult	mad	01/14/10-07/09/10	45	Cycling
Adult	mbi	01/25/10-07/09/10	47	Cycling
Adult	mdo	06/19/09-03/25/10	71	Cycling
Adult	min	10/11/09-04/20/10	35	Cycling
Adult	mki	02/06/10-07/09/10	41	Cycling
Adult	mos	02/09/10-06/28/10	29	Cycling
Adult	mzu	03/05/10-04/20/10	7	Cycling
Adult	pua	06/18/09-07/15/10	3	Cycling
Adult	pua	07/16/10-12/25/09	36	Pregnant
Adult	tit	02/20/10-07/09/10	23	Cycling
Adult	uvi	01/13/10-04/04/10	19	Cycling
Adult	yey	06/19/09-09/11/09	16	Cycling
Adult	yey	09/12/09-02/24/10	39	Pregnant
Adult	yey	06/01/10-07/10/10	14	Cycling
Adolescent	hod	07/13/09-04/20/10	75	Cycling
Adolescent	kad	07/20/09-02/23/10	53	Cycling
Adolescent	ten	07/20/09-04/17/10	73	Cycling

[1] The female disappeared for 30 days during this sampling period

Table 2.2. Summary of cycles for which sampling frequency during the period of maximum tumescence (MAX) allowed for the detection of the fecal estradiol (fE) surge,and hormone assay results, including the fE and fecal progesterone (fP) baseline, average fE levels during MAX, the highest fE value (i.e., the fE surge, used as a proxy for ovulation), and the highest fP values during the ovulatory window. The ovulatory window includes the day(s) fE rose above the fE surge threshold and was clearly higher than other fE values, plus the day(s) without samples on either side of it. Samples collected outside MAX include those collected after the end of deflation of the previous MAX until the end of deflation of the corresponding MAX period. See text for details.

Age class	**Female**	**Cycle ID**	**MAX duration (days)**	**# Samples during MAX**	**# Samples outside MAX**	**fE Baseline (ng/mg)**	**Average fE during MAX (ng/mg)**	**Highest fE value (ng/mg)**	**Ovulatory window**	**fP Baseline (ng/mg)**	**Highest fP (ng/mg)**	**Conceptive**
Adult	bad	1	6	3	9	252.1 ± 45.9	532.7 ± 265.6	816.4	Jul 31-Aug 3, 09	838.7 ± 156.6	2119.7	No
Adult	bad	5	5	4	9	252.1 ± 45.9	458.4 ± 75.1	550.3	Dec 11-12, 09	838.7 ± 156.6	2753.6	Yes
Adult	kim	1	8-10	5 or 6	4	381.1 ± 54.4	525.4 ± 260.6	910.0	Feb 14-16, 10	313.1 ± 43.4	1199.7	No
Adult	ksr	5	10-12	10	8	274.8 ± 62.3	503.3 ± 123.0	772.6	Nov 22-23, 09	784.0 ± 89.4	2302.9	No
Adult	kum	1	6	6	8	322.4 ± 42.4	368.6 ± 42.2	529.0	Jan 6-8, 10	794.9 ± 133.9	1599.1	No
Adult	kum	2	3	1	7	322.4 ± 42.4	673.0	673.0	Feb 9-11, 10	794.9 ± 133.9	888.3*	Yes
Adult	mbi	1	7	7	7	408.3 ± 50.1	488.1 ± 61.5	575.8	Anovulatory	587.5 ± 233.4	1288.8	No
Adult	mdo	3	7	7	12	308.8 ± 26.3	406.5 ± 95.7	540.5	Jan 24-27, 10	1070.8 ± 350.1	1556.4	No
Adult	mdo	4	11	6	2	308.8 ± 26.3	514.5 ± 137.2	673.4	Feb 16-19, 10	1070.8 ± 350.1	1733.9	Yes
Adolescent	hod	5	6-7	3	8	329.1 ± 45.6	470.0 ± 148.4	628.4	Jan 25-27, 10	491.8 ± 134.8	1587.7	No
Adolescent	kad	1	10	5	9	300.2 ± 37.4	445.64 ± 53.1	719.8	7-Nov-09	964.8 ± 321.6	2281.7	No
Adolescent	ten	3	7	3	13	318.9 ± 45.8	628.5 ± 126.2	769.7	Oct 30-Nov 1, 09	729.0 ± 189.2	1139.8	No

*Fecal progesterone peak during ovulatory window was below the fP threshold

Table 2.3. Characteristics of the menstrual cycle. Statistics [mean ± SD (range) N] were calculated using only cases known to the day.

	Age class & cycle type					
	Adult, non-conceptive		Adult, conceptive		Adolescent	
Parameter	Known to the day	Individual values known to within 1 or 2 days	Known to the day	Individual values known to within 1 or 2 days	Known to the day	Individual values known to within 1 or 2 days
Cycle length (m)[1]	30.0 ± 3.0 (27-33) 3	31-33 29-30	-	-	49.0 ± 6.3 (41-56) 5	56-58
Days from start of detumescence to start of bleeding[2]	5.7 ± 2.8 (1-11) 12	1-2 3-4 4-5 4-5 4-6 4-6 5-7 6-7 6-7	17.5 ± 0.7 (17-18) 2	3-4	4.8 ± 0.5 (4-5) 4	6-7 6-8
Bleeding duration[2]	6.6 ± 2.6 (2-10) 8	1-2 1-3 2-3 9-11 10-11 11-12	10.0 ± 1.4 (9-11) 2	-	9.2 ± 5.6 (3-16) 5	2-3 19-20

[1] m: calculated using menses

[2] Bleeding refers to menses (non-conceptive cycles and adolescent females) and implantation bleeding (conceptive cycles)

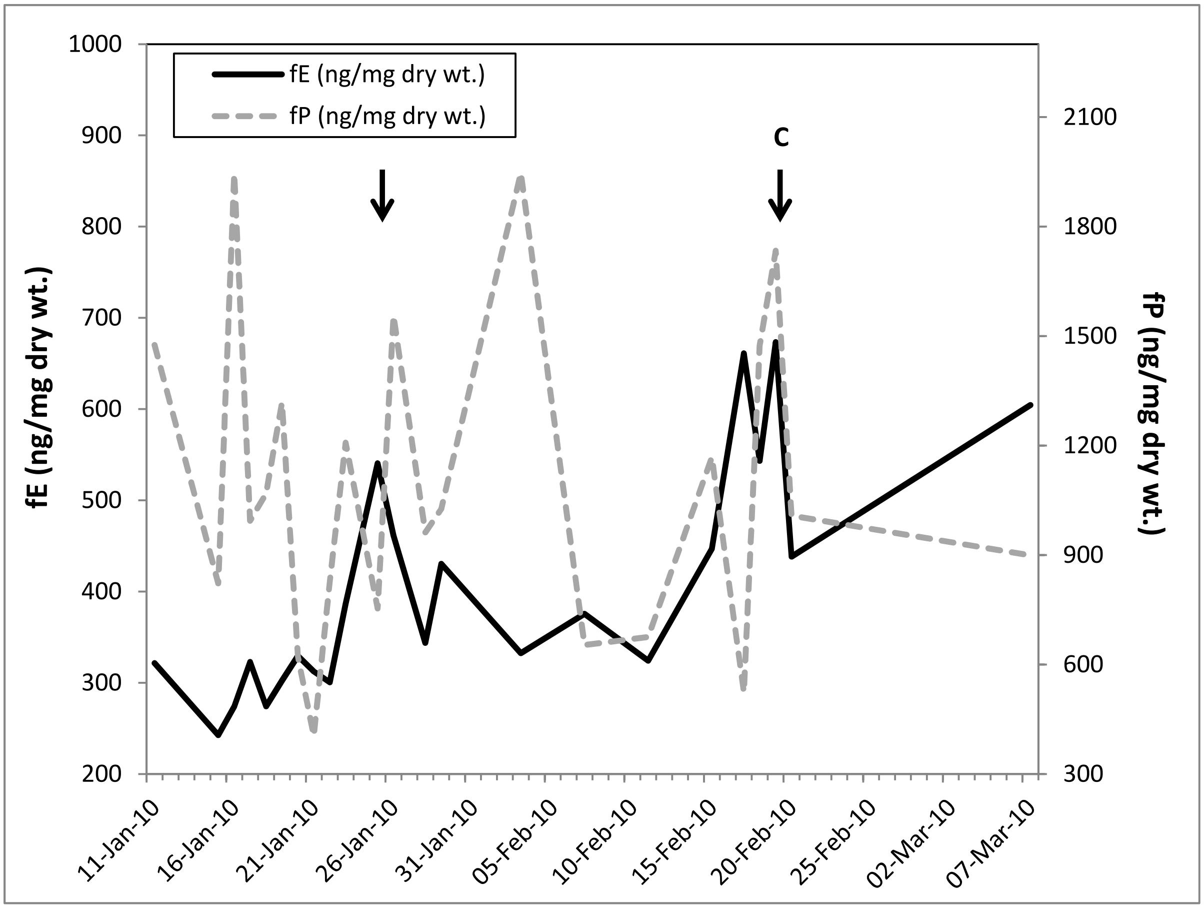

Figure 2.1. Fecal estradiol (fE, black line) and fecal progesterone (fP, dashed, grey line) for female 'mdo' during two consecutive ovulatory cycles depicting the difficulty interpreting the fP profile. Fecal progesterone remained elevated several days before the fE surge on January 26th, but it did not do so with the fE surge on February 19th. Low sampling frequency and fP value fluctuations also impeded the detection of fP after the January 26th fE surge. Arrows indicate the ovulatory fE peak. C: Conception

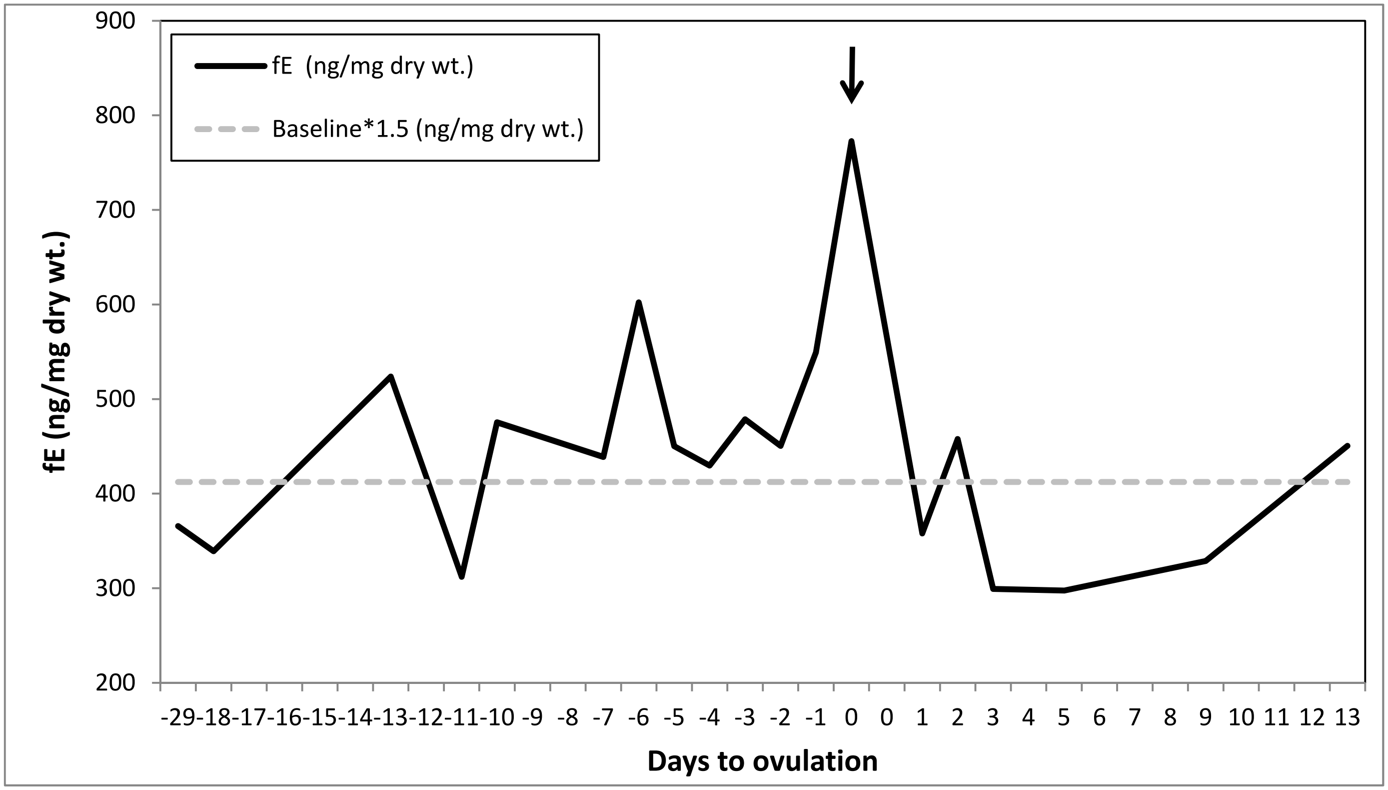

Figure 2.2. Fecal estradiol (fE) levels for one ovulatory cycle of female ksr, showing the fE surge (presumed ovulation, arrow, day 0 (arrow). Dashed, grey line indicates the ovulatory threshold, defined as the baseline (274.8 ng/mg dry wt.) multiplied by 1.5. See text for more details.

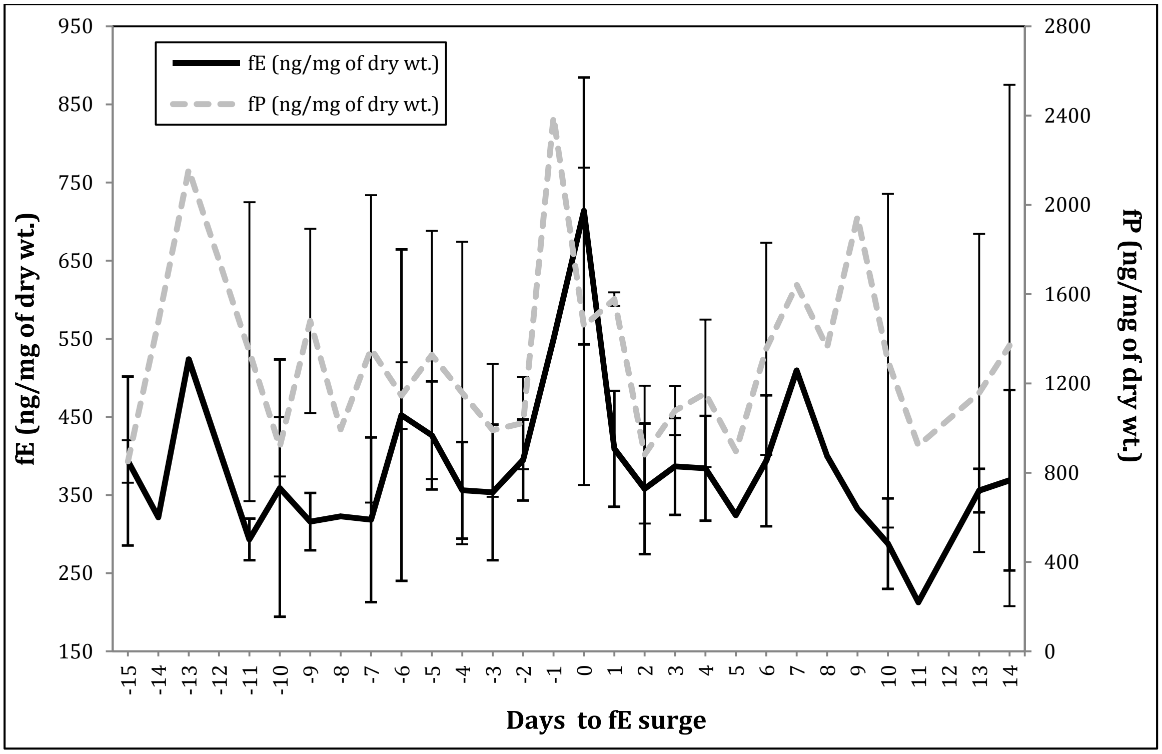

Figure 2.3. Composite profile illustrating mean fecal estradiol (fE) ± SD and mean fecal progesterone (fP) for five ovulatory, non-conceptive cycles (N = 5 females). 0: day of fE surge, used as a proxy for ovulation.

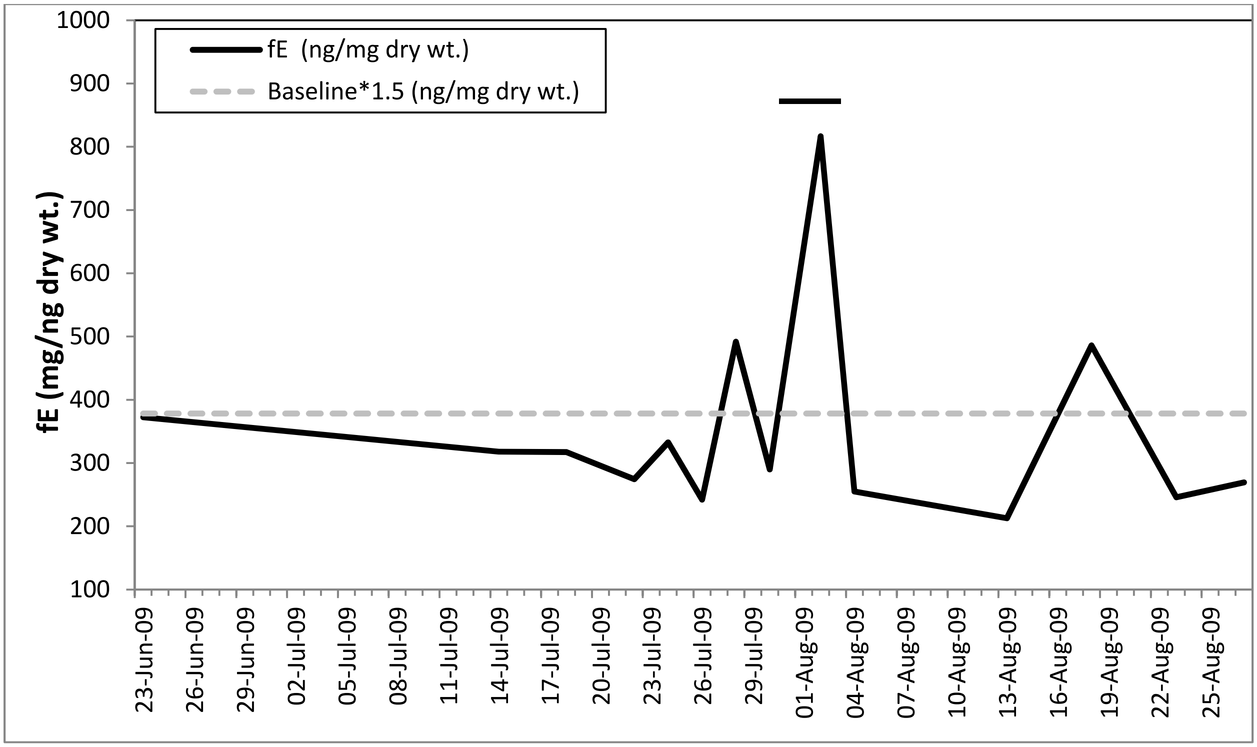

Figure 2.4. Fecal estradiol (fE) profile for cycle bad1. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (252.1 ng/mg dry wt.) multiplied by 1.5. See text for more details.

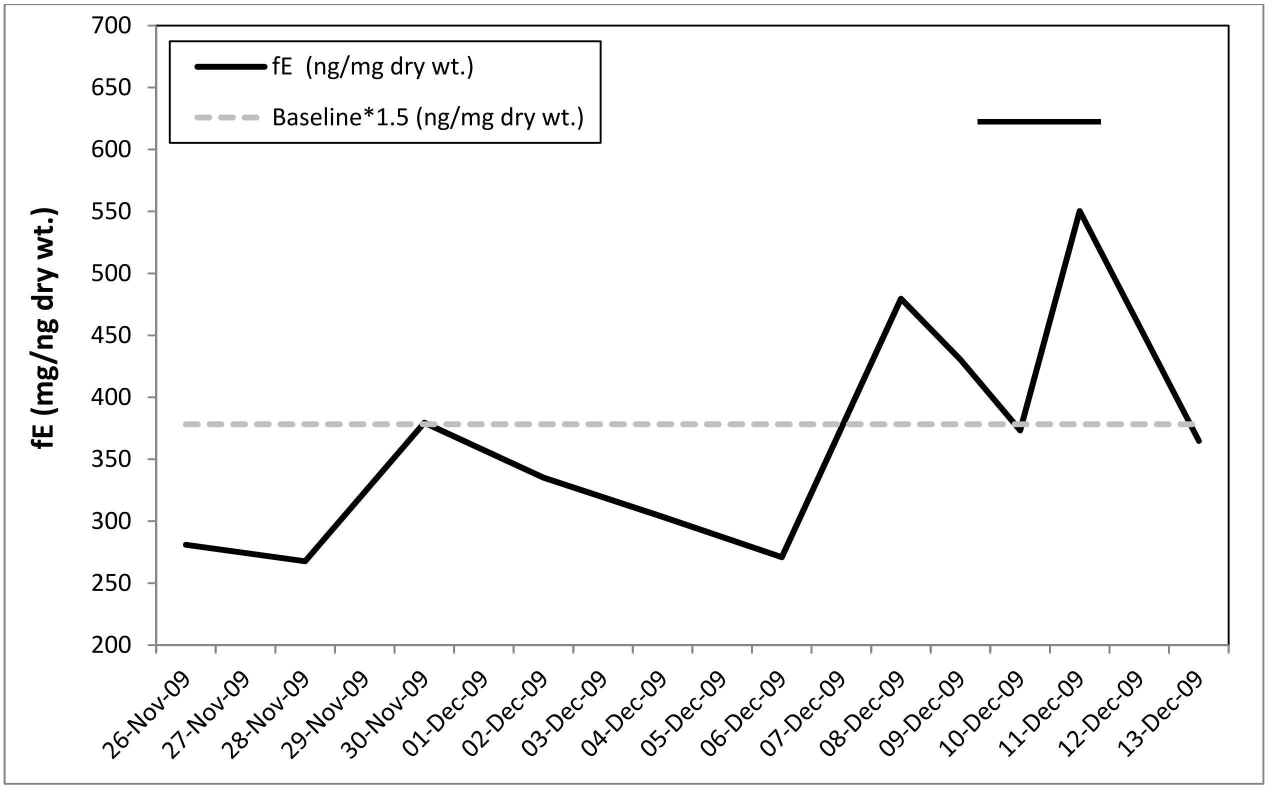

Figure 2.5. Fecal estradiol (fE) profile for cycle bad5. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (252.1 ng/mg dry wt.) multiplied by 1.5. See text for more details.

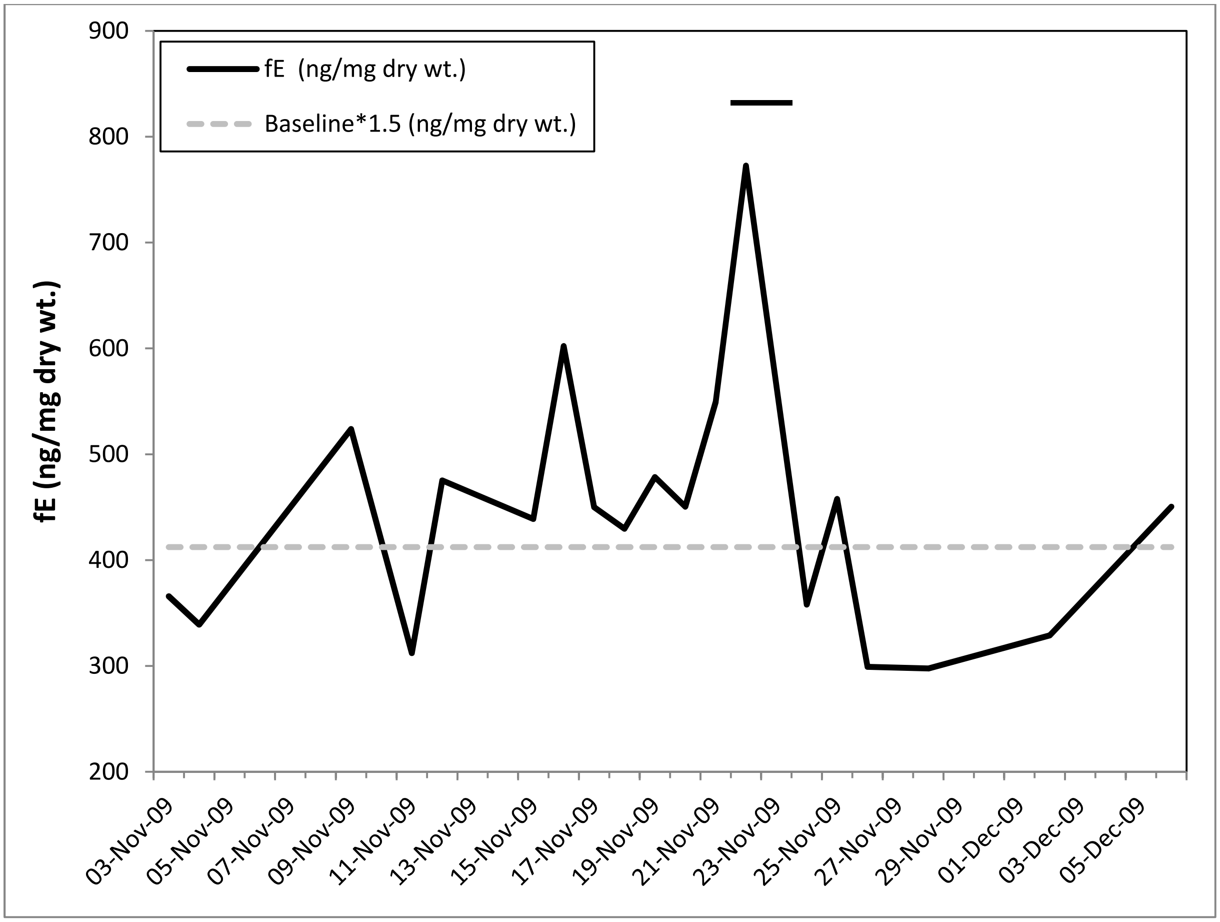

Figure 2.6. Fecal estradiol (fE) profile for cycle ksr5. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (274.8 ng/mg dry wt.) multiplied by 1.5. See text for more details.

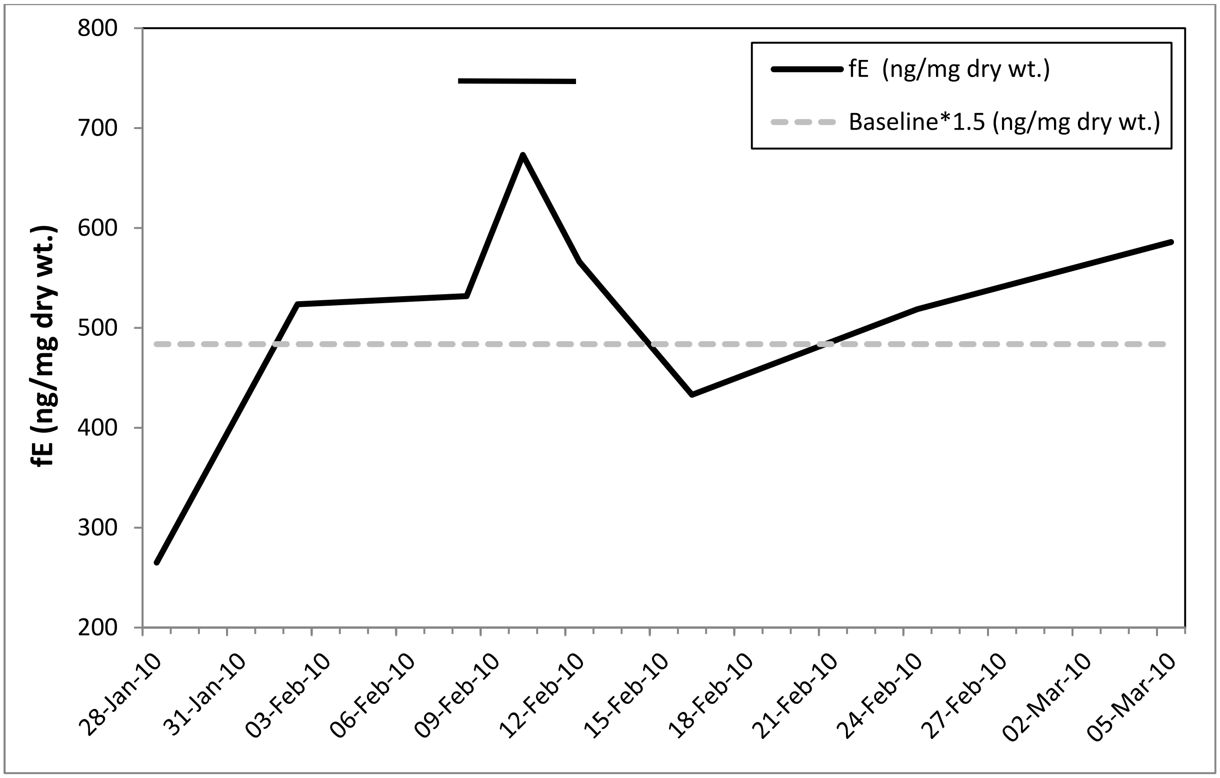

Figure 2.7. Fecal estradiol (fE) profile for cycle kum2. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (322.4 ng/mg dry wt.) multiplied by 1.5. See text for more details.

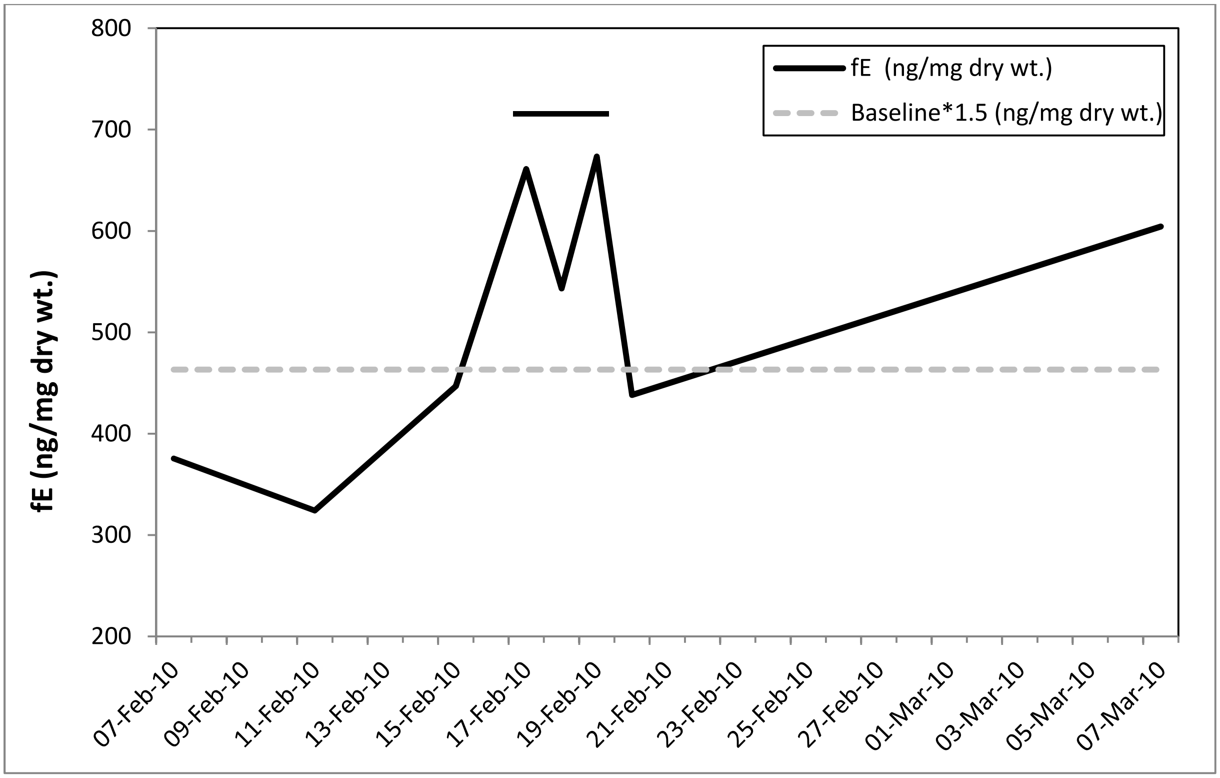

Figure 2.8. Fecal estradiol (fE) profile for cycle mdo4. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (308.8 ng ng/mg dry wt.) multiplied by 1.5. See text for more details.

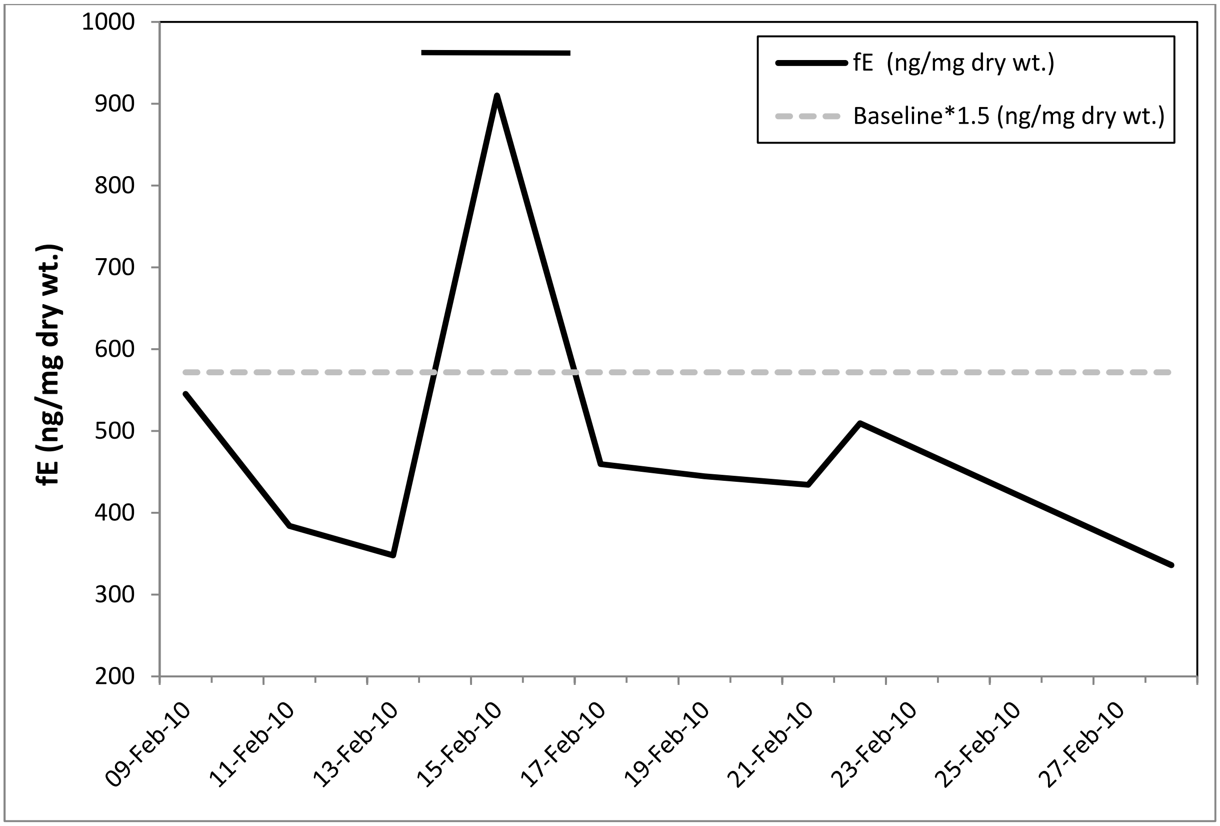

Figure 2.9. Fecal estradiol (fE) profile for cycle kim1 Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (381.1 ng/mg dry wt.) multiplied by 1.5. See text for more details.

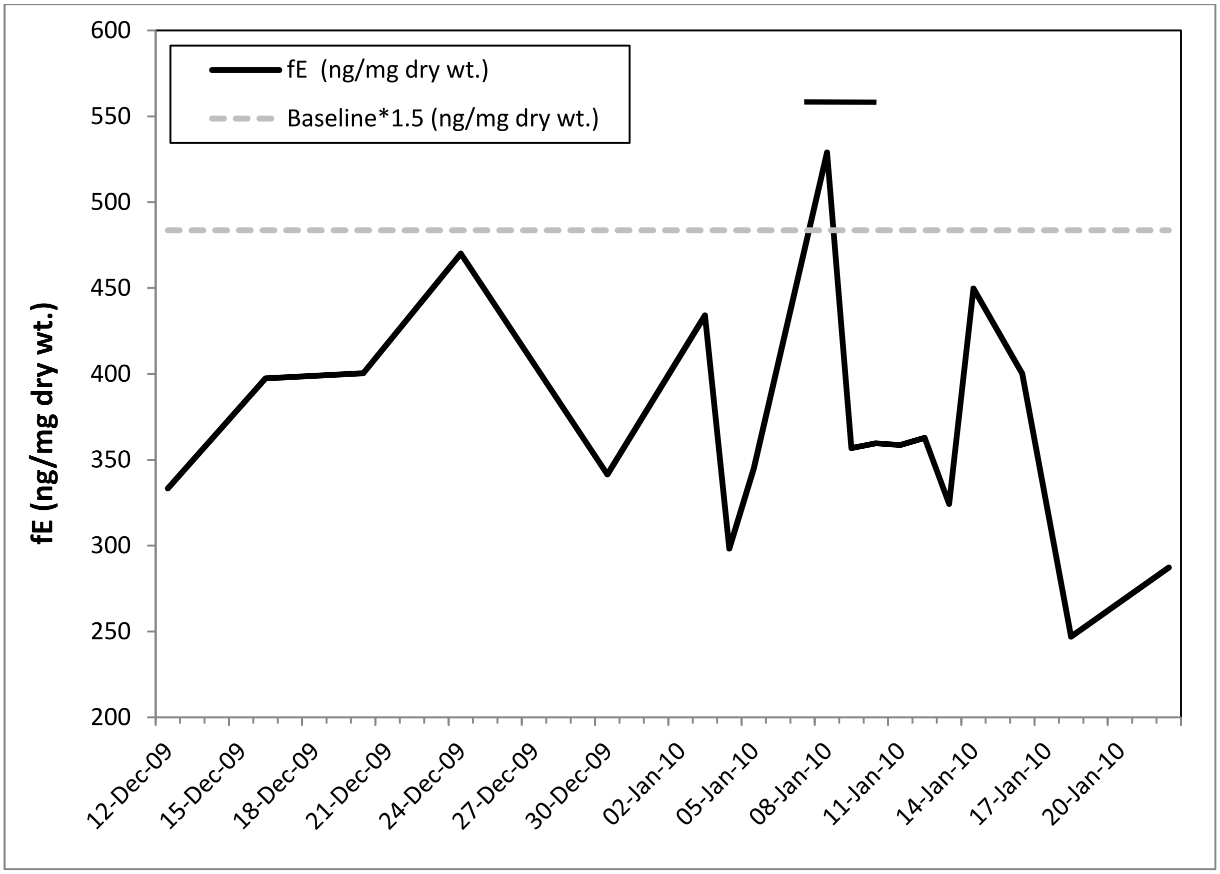

Figure 2.10. Fecal estradiol (fE) profile for cycle kum1. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (322.4 ng/mg dry wt.) multiplied by 1.5. See text for more details.

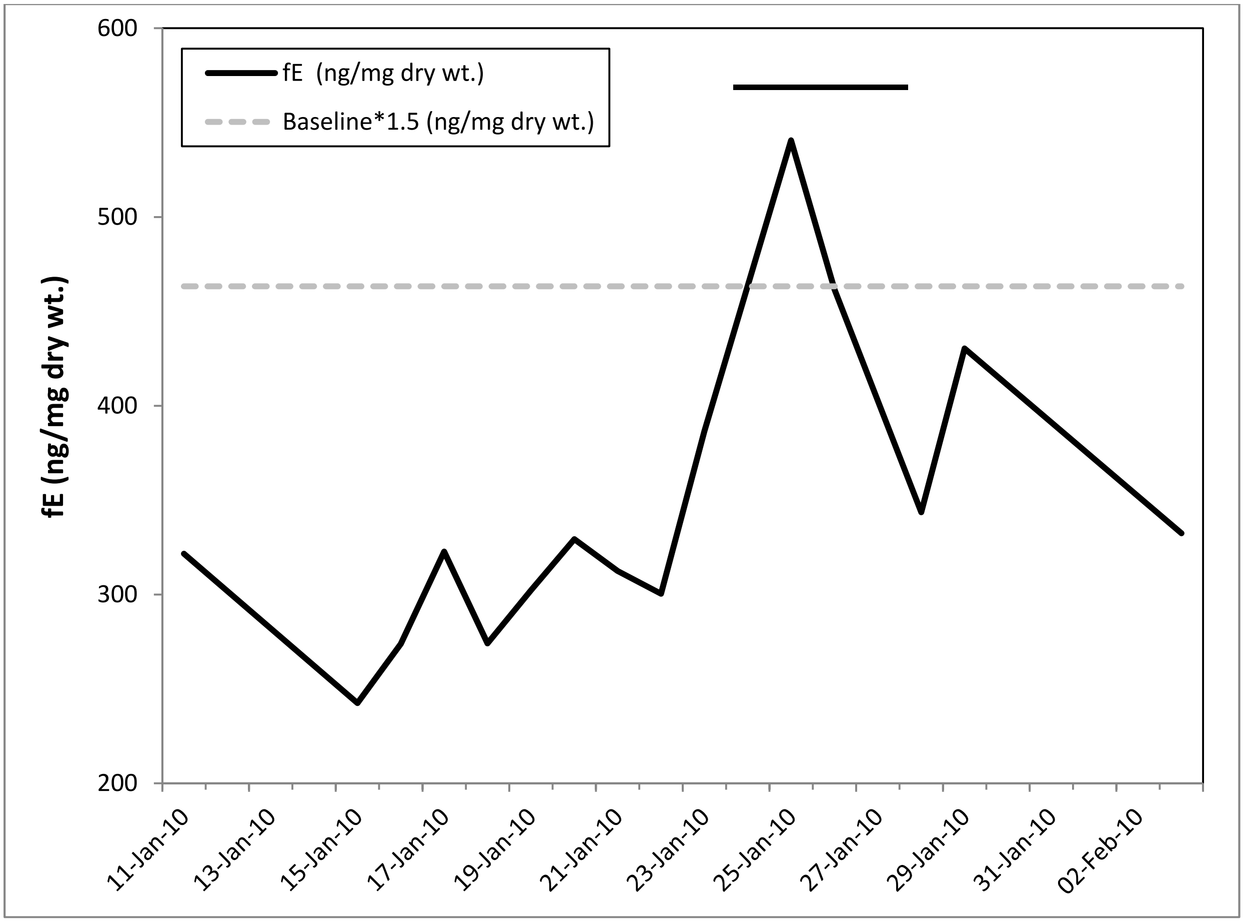

Figure 2.11. Fecal estradiol (fE) profile for cycle mdo3. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (308.8 ng ng/mg dry wt.) multiplied by 1.5. See text for more details.

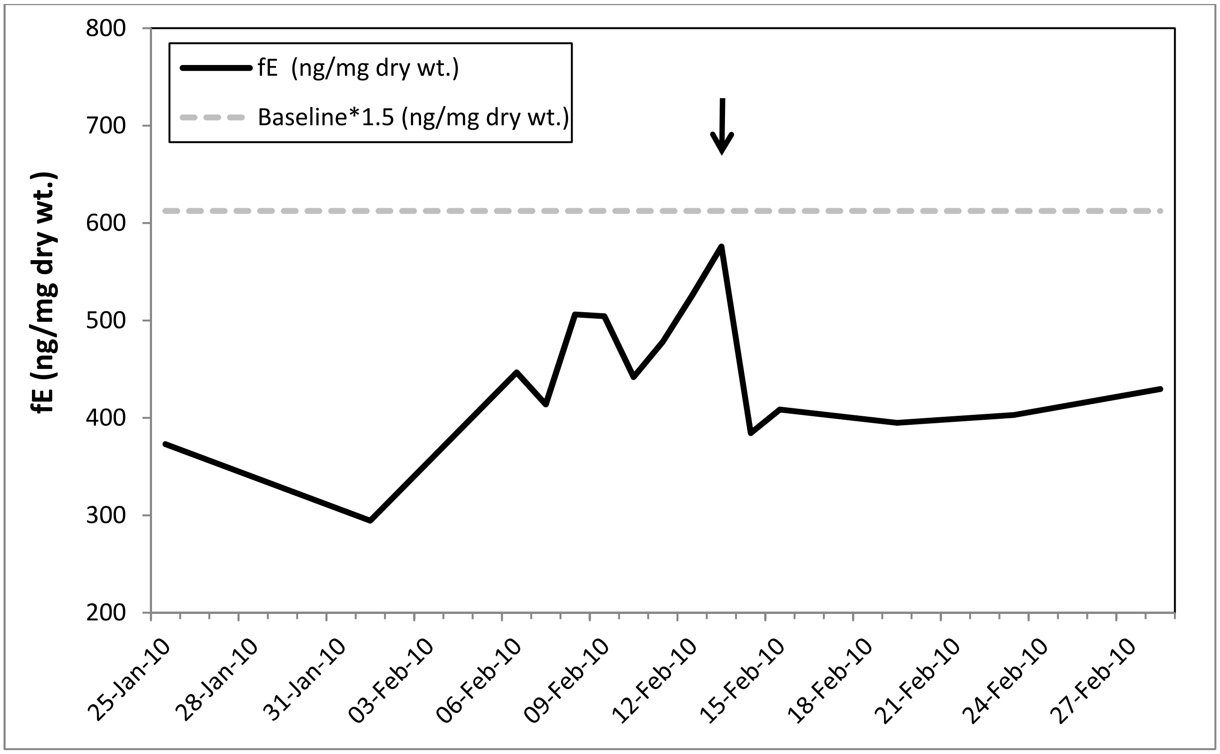

Figure 2.12. Fecal estradiol (fE) profile for cycle mbi1. The highest fE value reached during this cycle (arrow) was below the fE surge threshold, defined as the baseline (408.3 ng/mg dry wt.) multiplied by 1.5, and thus was considered anovulatory. See text for more details.

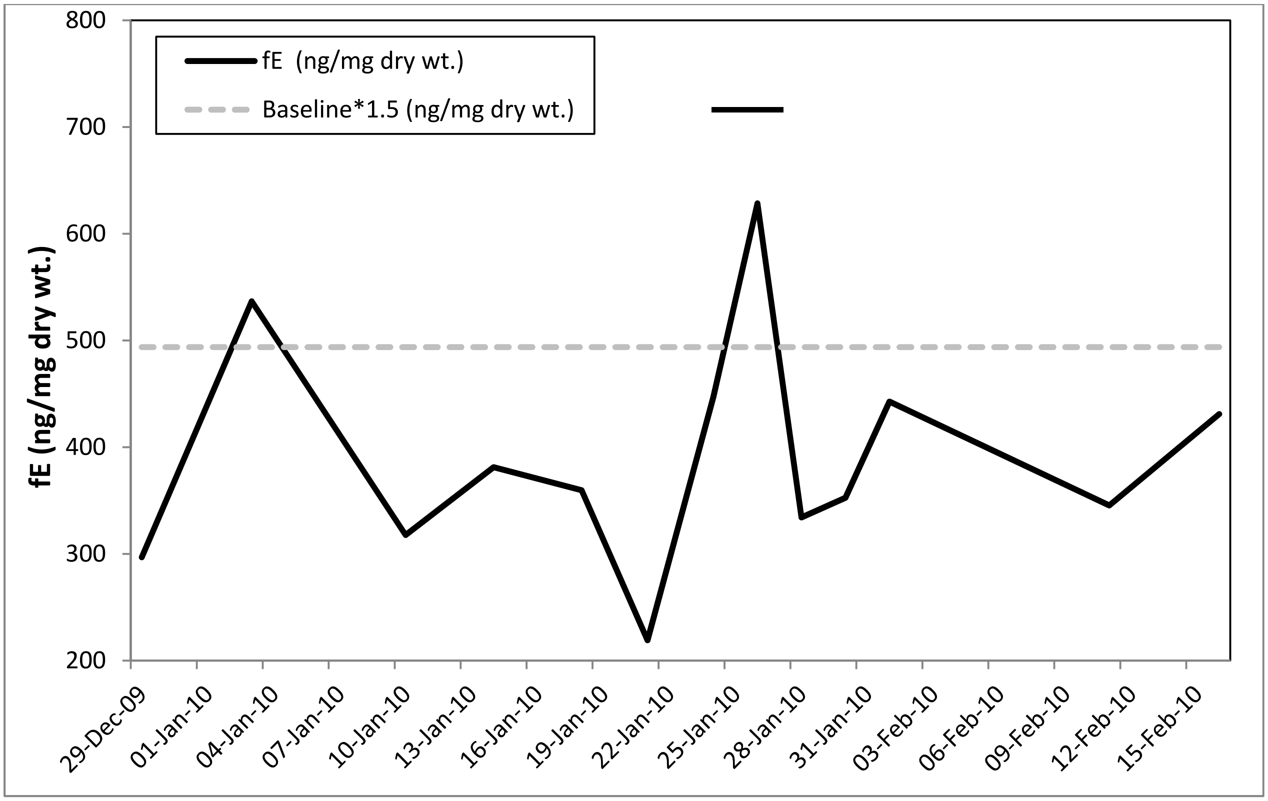

Figure 2.13. Fecal estradiol (fE) profile for cycle of hod5, an adolescent female. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (329.1 ng ng/mg dry wt.) multiplied by 1.5. See text for more details.

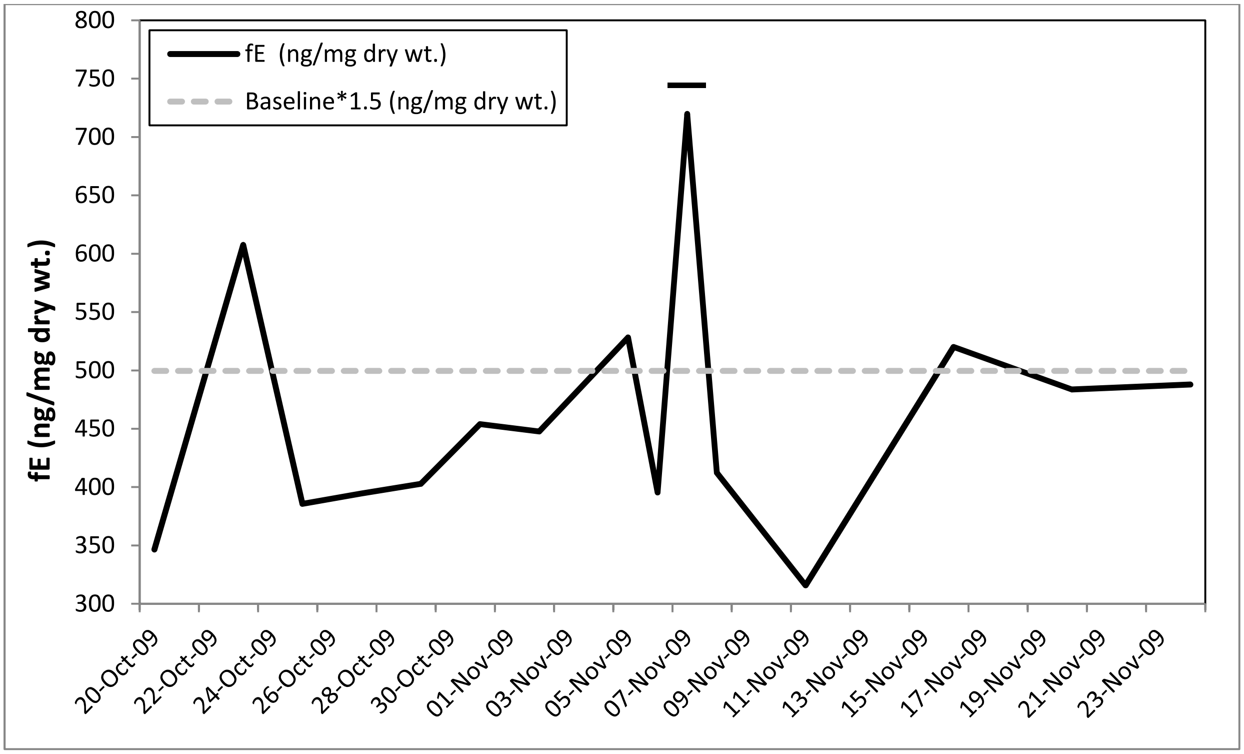

Figure 2.14. Fecal estradiol (fE) profile for cycle of kad1, an adolescent female. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (333.0 ng ng/mg dry wt.) multiplied by 1.5. See text for more details.

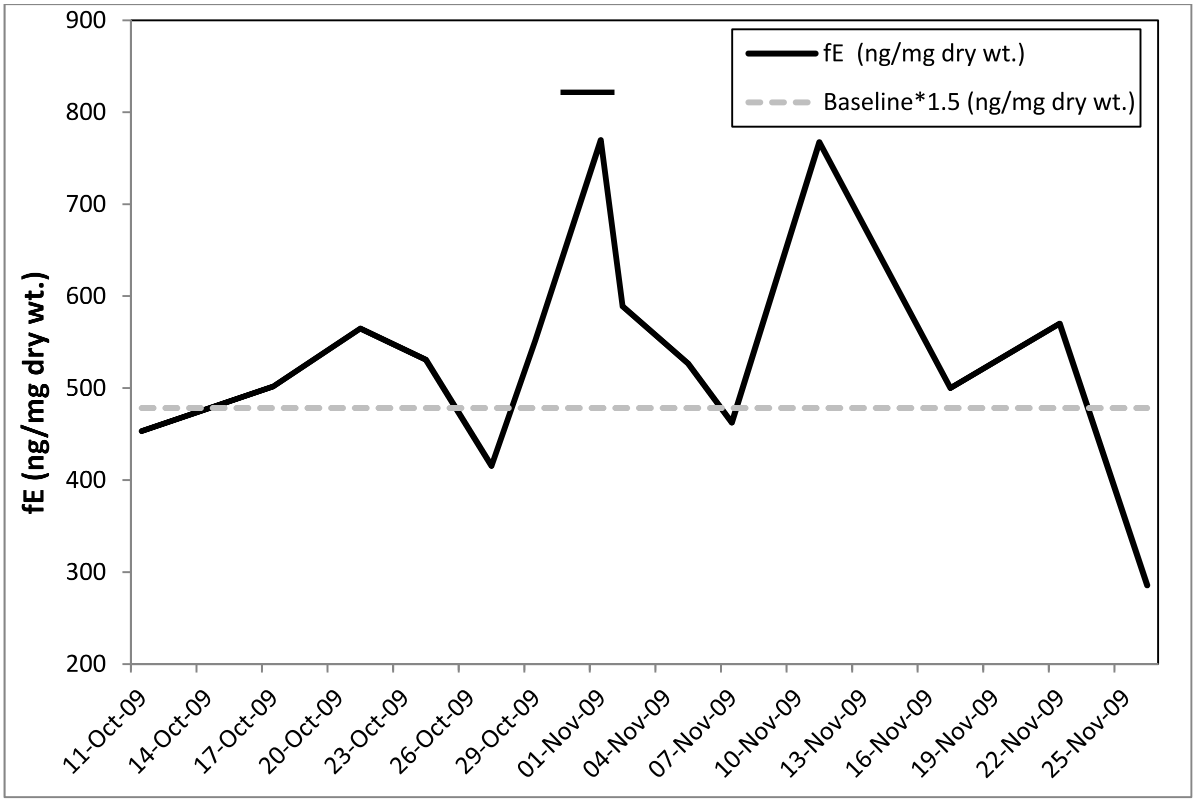

Figure 2.15. Fecal estradiol (fE) profile for cycle of ten3, an adolescent female. Solid, horizontal bar indicates the ovulatory window. Dashed, grey bar indicates the fE surge threshold, defined as the baseline (318.9 ng ng/mg dry wt.) multiplied by 1.5. See text for more details.

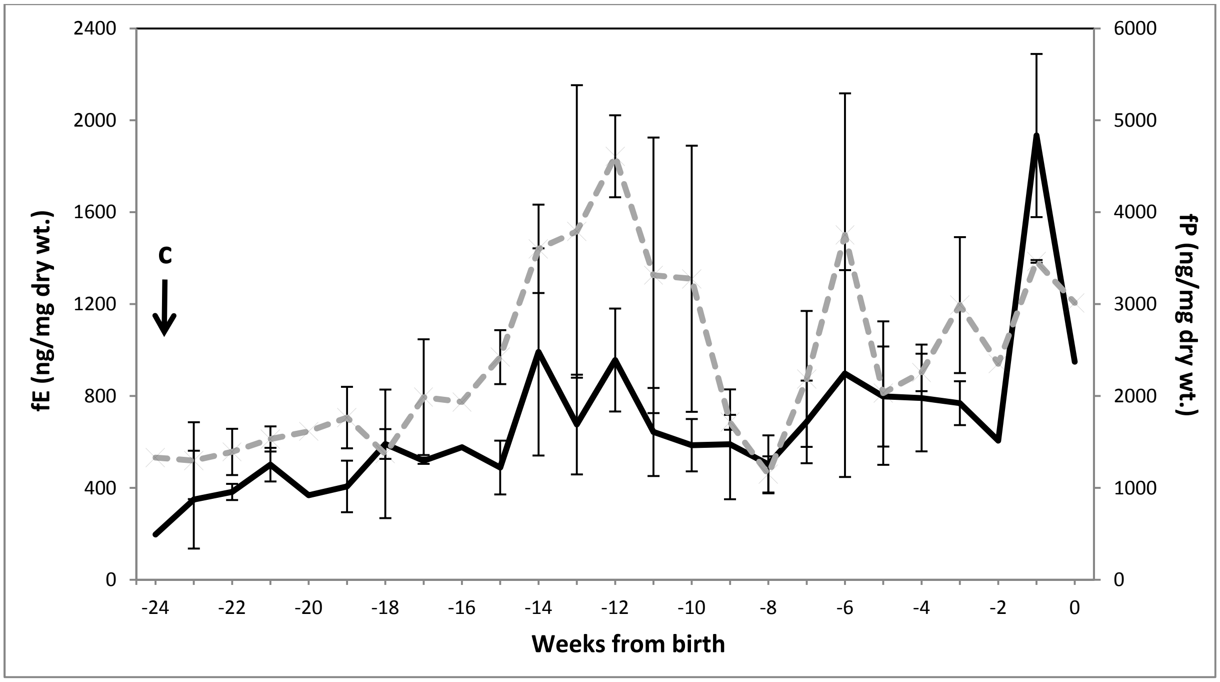

Figure 2.16. Composite profile illustrating mean fecal estradiol (fE) ± SD and fecal progesterone (fP) for two gestations. C: conception; 0: birth.

CHAPTER THREE:

SEXUAL SWELLINGS OF WILD SANJE MANGABEYS (*CERCOCEBUS SANJEI*): CHANGES IN TUMESCENCE AND APPEARANCE IN RELATION TO SWELLING TYPE, FEMALE AGE, AND THE TIMING OF OVULATION

*To be submitted under the title 'Sexual swellings of wild Sanje mangabeys (*Cercocebus sanjei*): changes in tumescence and appearance in relation to relation female age, swelling type and the timing of ovulation' by David Fernández, Diane Doran-Sheehy, Carola Borries, and Carolyn L. Ehardt.*

Abstract

Females of numerous catarrhine primates exhibit exaggerated sexual swellings during the menstrual cycle that peak in size (maximum tumescence or MAX) around the time of ovulation. Among the hypotheses proposed to explain their functional significance, the graded-signal hypothesis has received the most support to date. This hypothesis states that sexual swelling size functions as a probabilistic signal, revealing when ovulation is most likely to occur, but not the exact timing. Sexual swellings may also differ based on the swelling type and female age, and thus provide information on female fertility. Here we used behavioral observations to describe changes in the tumescence and appearance of the sexual swellings of wild Sanje mangabeys (*Cercocebus sanjei*) (N = 18 adult females, 3 adolescent females) and their relationship to fecal estradiol (fE) concentrations to test whether they are consistent with the graded-signal hypothesis. In addition, we compared different sexual swelling types (first swelling post-partum, first swelling after infant death, swelling during non-conceptive and conceptive cycles, and post-conceptive swelling) and age-class (adult and adolescent) to examine if they can provide visual cues to males regarding female fertility. During non-conceptive cycles, swellings displayed MAX an average (± SD) of 6.5 ± 2.4 days. During that time, the appearance of the sexual swellings changed, becoming brighter (i.e., the 'shiny phase') for an average of 4.0 ± 1.7 days. In all cases (N = 7 swellings), the fE surge, used as a proxy for ovulation, occurred during MAX, most frequently during the second half. Moreover, in 83.3% of the cases (N = 6 swellings), the fE surge occurred the day immediately after the onset of the shiny phase. Compared to non-conceptive swellings, conceptive swellings had shorter shiny phases (1.7 ± 1.2 days), a difference that approached significance (Mann-Whitney U: z = -1.909, p = 0.070). The first swelling post-partum tended to have shorter MAX periods compared to swellings during later cycles (4.8 ± 2.4 days; Mann-Whitney U: z = 1.810, p = 0.070). Post-conceptive swellings were less likely to undergo a shiny phase (25% of swellings, N = 4). Adolescent females displayed significantly longer shiny phases (6.4 ± 2.7 days) compared to swellings during non-conceptive (Mann-Whiney U: z = 2.403, p = 0.012) and conceptive (Mann-Whiney U: z = 2.702, p = 0.006) cycles of adults. Overall, our results are consistent with the graded signal hypothesis, and suggest that in this species sexual swellings may provide males with information on the timing of ovulation, swelling type and female age. The analysis of male sexual behavior will ultimately confirm what information is conveyed to males regarding female fertility through sexual swellings.

Keywords: adolescent, cycle quality, graded-signal, paternity confusion, paternity concentration, post-conceptive swelling, Udzungwa Mountains

Introduction

Females of numerous catarrhine primates exhibit exaggerated sexual swellings that change in size and coloration during the menstrual cycle, as well as with the female's age and reproductive state (Dixson, 1983; 2012). In these species, the skin around the vulvar and/or anal region swells and shrinks during the menstrual cycle in response to fluctuations in ovarian hormone levels, peaking in size around the time of ovulation (Dixson, 1983). In particular, estradiol induces tumescence, while progesterone triggers detumescence (Zuckerman, 1937; Gillman, 1940). Such sexual swellings have been associated with primates living in multi-male mating systems, in which females may have multiple mating partners (Clutton-Brock and Harvey, 1976), and with species that lack a distinct breeding season (van Schaik et al., 2001).

Several hypotheses have been proposed to explain the evolution and function of sexual swellings (the best-male hypothesis: Clutton-Brock and Harvey, 1976; the many-male hypothesis: Hrdy, 1981; Hrdy and Whitten, 1987; the obvious-ovulation hypothesis: Hamilton, 1984; the male services hypothesis: van Noordwijk, 1985; the reliable indicator hypothesis: Pagel, 1994; the graded-signal hypothesis: Nunn, 1999; the differentiating between cycles hypothesis: Zinner et al., 2002; Emery and Whitten, 2003, the paternal care hypothesis: Alberts and Fitzpatrick, 2012; see Nunn 1999 for a review). These hypotheses are not mutually exclusive, and as noted by Alberts and Fitzpatrick (2012), they frequently address different levels of variation in sexual swelling size. For example, most hypotheses address variation within a single cycle, typically whether maximum swelling size signals the timing of ovulation within the menstrual cycle (the best-male hypothesis: Clutton-Brock and Harvey, 1976; the many-male hypothesis: Hrdy, 1981; Hrdy and Whitten, 1987; the obvious-ovulation hypothesis: Hamilton, 1984; the male services hypothesis: van Noordwijk, 1985; the graded-signal hypothesis: Nunn, 1999). Others consider whether variation in swelling size between cycles of the same female conveys information, such as the probability of conception (the differentiating between cycles hypothesis: Zinner et al., 2002; Emery and Whitten, 2003), while some test whether variation in swelling size among females provides information about the quality (e.g., physical condition) of a particular female (the reliable indicator hypothesis: Pagel, 1994).

Most hypotheses focusing on variation in sexual swelling size during the menstrual cycle have proposed that sexual swellings function to indicate when ovulation occurs, and predict it will occur when the swelling is largest (Dixson, 1983). Among them, the graded-signal hypothesis (Nunn, 1999) has received the most support to date (bonobos, *Pan paniscus*: Reichert et al., 2002; chimpanzees, *P. troglodytes verus*: Deschner et al., 2003; 2004; long-tailed macaques, *Macaca fascicularis*: Engelhardt et al., 2005; Barbary macaques, *M. sylvanus*: Möhle et al., 2005; Brauch et al., 2007; olive baboons, *Papio anubis*: Higham et al., 2008a; b). This hypothesis proposes that sexual swellings function as a probabilistic signal, with the probability of ovulation highest during the period of maximum tumescence (MAX), and with decreasing probabilities before and after MAX (Nunn, 1999). Sexual swellings, therefore, enable both concentration and confusion of paternity (Nunn, 1999). In particular, the more precise swellings are at indicating ovulation, the more likely that the male with the highest competitive ability (i.e., the ‘best’ male) can monopolize paternity through mate guarding. By maximizing their chances of conceiving with the best male, females may be gaining genetic benefits (Nunn, 1999). Conversely, when the swellings are less precise at indicating ovulation, females have more opportunities to increase the number of mating partners and confuse paternity (Nunn, 1999). Females would benefit, therefore, by gaining additional paternal support from the males with whom they have mated when the probability of ovulation was lower, e.g., males willing to protect them and their offspring from predators and attacks by conspecifics (Taub, 1980; Hrdy, 1981; van Noordwijk, 1985; Harvey and May, 1989; Palombit et al., 1997; Borries et al., 1999).

Most studies that have examined the relationship between ovulation and sexual swelling size have found support for the graded signal hypothesis. In most cases, ovulation occurred during MAX (baboons: Wildt et al., 1977; Shaikh et al., 1982; Higham et al., 2008a; b; Daspre et al., 2009; sooty mangabeys, *Cercocebus atys*: Aidara et al., 1981; Whitten and Russell, 1996; bonobos: Reichert et al., 2002; chimpanzees: Deschner et al., 2003; Emery and Whitten, 2003; Deschner et al., 2004; long-tailed macaques: Engelhardt et al., 2005; Barbary macaques: Möhle et al., 2005; Brauch et al., 2007), and most frequently during the second half, just prior to detumescence (bonobos: Reichert et al., 2002; chimpanzees: Deschner et al., 2003; long-tailed macaques: Engelhardt et al., 2005; baboons: Higham et al., 2008a; Daspre et al., 2009). For example, evidence from laparoscopic examinations of baboons revealed that the majority of ovulations occurred within five days prior to the start of detumescence (56.3% of cycles: Wildt et al., 1977; 96.5% of cycles: Shaikh et al., 1982). In a few studies, however, ovulation has been documented either before (sooty mangabeys: Whitten and Russell, 1996) or after MAX (baboons: Wildt et al., 1977; Shaikh et al., 1982; Reichert et al., 2002; Daspre et al., 2009; sooty mangabeys: Whitten and Russell, 1996). What varies among species, therefore, is how precise the relationship is between sexual swelling size and ovulation, which Alberts and Fitzpatrick (2012) have explained as a trade-off between concentrating and confusing paternity.

Sexual swellings may also differ and thus provide information on the swelling type a female is undergoing and on differences that are due to female age. For example, females typically require several cycles to conceive following the period of post-partum amenorrhea (e.g., Altmann et al., 1978; Chapter 2) and some studies have found that swelling size increases as the female undergoes successive cycles (Emery and Whitten, 2003; Deschner et al., 2004; Higham et al., 2008b; Huchard et al., 2009). In such cases, conceptive swellings have been found to be larger than non-conceptive swellings (Alberts et al., 2006; Gesquiere et al., 2007; Daspre et al., 2009; Higham et al., 2012), potentially providing males with signals to distinguish among females undergoing these two cycle types (Bulger, 1993; Weingrill et al., 2003; Daspre et al., 2009; but see Setchell and Wickings, 2006). Swellings may also advertise female age-class, as adolescent females usually undergo a period of sterility during which they experience a series of irregular, anovulatory cycles before conceiving (Hartman, 1931; reviewed in Dixson, 2012). During this time, their swellings are larger and more brightly colored than those of adults (reviewed in Anderson and Bielert, 1994), which may function as a signal that males use to discriminate among females. Studies indicate that males appear to prefer mating with adults over adolescent females (Bielert and Anderson, 1985), suggesting that they can distinguish the swelling of an adolescent from that of an adult (Anderson and Bielert, 1994). Finally, in some species, females develop sexual swellings during gestation (e.g., pig-tailed macaques: Hadidian and Bernstein, 1979; chimpanzees: Wallis, 1982; long-tailed macaques: van Noordwijk, 1985; Tana river mangabeys, *C. galeritus*: Kinnaird, 1990; sooty mangabeys: Gordon et al., 1991; mandrills, *Mandrillus sphinx*: Bettinger et al., 1995; Barbary macaques: Möhle et al., 2005). As conception is not possible at this time, it has been argued that these post-conceptive swellings function to further confuse paternity, thereby reducing the risk of infanticide and increasing the potential for paternal investment (Hrdy, 1979; Hrdy and Whitten, 1987). This would only be an effective strategy, however, if males were unable to distinguish between the sexual swellings of pregnant and non-pregnant females, which does appear to be the case in some species (Barbary macaques:

Small, 1990; long-tailed macaques: Engelhardt et al., 2007), but not in others (Barbary macaques: Küster and Paul, 1984; sooty mangabeys: Gordon et al., 1991; Gust, 1994).

Here we investigate the sexual swellings and hormonal profiles of wild Sanje mangabeys (*Cercocebus sanjei*), an African cercopithecine that exhibits a multi-male mating system and exaggerated sexual swellings. As the sexual swellings of *Cercocebus* mangabeys have only been described for two species, the sooty and the golden-bellied mangabey (Aidara et al., 1981; Whitten and Russell, 1996; Walker et al., 2004), we being by providing a quantitative description of the changes in tumescence and appearance of the sexual swelling in cycling adult females. In particular, we describe the duration of the periods of inflation, MAX, and deflation that contribute to cycle length. We document a change of coloration and texture in the sexual swelling that occurs during maximum swelling; i.e., the "shiny phase", when the sexual skin acquires a darker and shinier tone. We then examine the function of sexual swellings by comparing our visual estimates of swelling tumescence and appearance with analyses of fecal estradiol metabolites (fE). If sexual swellings in Sanje mangabeys are consistent with the graded-signal hypothesis, we predict that the fE surge indicative of ovulation (Saltzman et al., 2010; Chapter 2) will occur more frequently during MAX, and more specifically, during the last five days prior to the onset of detumescence (Wildt et al., 1977; Shaikh et al., 1982). We will also examine how the shiny phase relates to the timing of the fE surge, and thus, if it provides an additional signal of female fertility to the male. Finally, if sexual swellings provide accurate visual cues about the swelling type a female is undergoing and/or female age, we predict that the duration of MAX and appearance of the shiny phase will differ with the adult female's swelling type (first swelling post-partum, first swelling after infant death, swelling during adult non-conceptive and conceptive cycles, and post-conceptive swelling), as well as between adult and adolescent females.

Methods

Study site and subjects

The study was conducted on one habituated group of Sanje mangabeys inhabiting the Mwanihana Forest (7°40'–7°57'S, 36°46'–36°56'E) of the Udzungwa Mountains National Park, Tanzania. The habitat is a mosaic of montane and sub-montane tropical forest, interspersed by areas of deciduous primary and secondary vegetation (Lovett, 1993; Ehardt et al., 2005). Annual rainfall in the Udzungwa Mountains averages 1,750 mm/year (Lovett, 1996), with a clear rainy season from November to May that receives the majority of rain (McCabe, 2012). Sanje mangabeys mate and give birth throughout the year; however, most conceptions occur from January through March (McCabe, 2012).

The study group, the Mizimu group, was first habituated in 2004 and has been monitored regularly ever since (Ehardt et al., 2005; Ehardt, unpublished). During the study, the group consisted of 63-65 individuals, including seven to ten adult males, 18 to 20 adult females, three adolescent females, as well as juveniles and infants. All adult and cycling adolescent females were identified using scars and facial coloration. Adolescent females were distinguished from adults by their relatively larger and brighter sexual swellings (Anderson and Bielert, 1994), smaller body size (Sigg et al., 1982), button-like nipples (Altmann et al., 1977), and lighter colored facial skin. Adolescents underwent a period of sterility (Hartman, 1931; Dixson, 2012), cycling for up to 16 months without conceiving (Chapter 2), and none of the adolescents conceived during the study period. Data presented here refer to 18 adult and three adolescent females.

Data collection

Data collection can be divided into two periods according to the type of data gathered (see below): Period 1 (Oct. 13, 2008 - May 1, 2009) and Period 2 (Jun. 11, 2009 – Jul. 10, 2010). Data collection tasks were divided among myself, and my research team: Clever P. Ngatwika (Oct. 13, 2008 - Apr. 5, 2010), Aly C. Mihambo (Oct. 13, 2008 – Nov. 13, 2009), Bakari S. Ponda (Mar. 14, 2009 – Jul. 10, 2010), Francis J. Masinde (Aug. 11, 2009 - May 8, 2010) and Aloyce M. Kigoma (Apr. 11, 2010 – Jul. 10, 2010). Every four months we conducted inter-observer reliability tests to ensure consistency in data collection among the different observers, requiring an agreement of at least 90% (Martin and Bateson, 2007). Whenever the group was followed (N = 408 days), it was contacted at the sleeping site and followed all day until the group reached the new sleeping site at night. The exception was two days during Period 2, in which we lost contact with the group for 1.3 and 1.6 hours, respectively.

During Period 1, the group was followed a mean of 8.8 ± 4.3 days per month (range: 4 – 18, total = 70 days). During Period 2, the group was followed an average of 23.1 ± 6.0 days/month (range: 10 – 30, for a total of 338 days or 3,346.4 hours (10.36 ± 1.2 hours/observation day).

Sexual swelling tumescence and appearance scoring

We began collecting data on sexual swelling size during Period 1 once females could be reliably identified (completed on Dec. 1, 2008) and continued for the duration of Period 2. We began collecting data on presence of the shiny phase in Sept. 2009. Each day the group was followed, we (myself, CPN, ALC, FJM, AMK) collected sexual swelling size and appearance using a 9-point scale, modified after Whitten and Russell (1996) and Walker et al. (2004) (Table 3.1). Swellings were then categorized into one of four states based on their scores. These included: 1) the absence of any sexual swelling (score 0); 2) a sexual swelling increasing in tumescence, i.e., inflation (scores 1 to 4); 3) MAX (score 5); and 4) a sexual swelling decreasing in tumescence, or the period of detumescence, i.e., deflation (scores 6 to 8) (Table 3.1; Figure 3.1). The scale was designed to capture relative, rather than absolute, changes in the tumescence of the swelling; therefore, two females may have the same swelling score (e.g., score 5) but one may display a sexual swelling of larger absolute size. In addition, each day of MAX we also scored the presence or absence of the shiny phase, which gave the swelling a shinier, brighter tone, as if covered with a thin oil film. The presence of the shiny phase, previously undescribed for mangabeys, was a very conspicuous trait, easy to detect and with high inter-observer agreement. We did not observe any changes in the coloration of the sexual skin.

Female reproductive state

We divided females into three reproductive states (cycling, pregnant, or post-partum amenorrhea) based on changes in sexual swelling size and on records of infant births, nipple contact and deaths, which were recorded daily throughout Periods 1 and 2. Cycling females underwent successive inflations and deflations, reaching MAX approximately every 30 days (Hadidian and Bernstein, 1979; Whitten and Russell, 1996; Walker et al., 2004). Females were classified as pregnant when they stopped cycling and developed a post-conceptive swelling which reached MAX approximately 50 days after the last MAX period (i.e., the conceptive cycle), as described for other *Cercocebus* (Hadidian and Bernstein, 1979; Kinnaird, 1990; Gust, 1994; Walker et al., 2004). Gestations were ultimately confirmed hormonally (Chapter 2) and/or with the birth of an infant approximately 173 days after conception, the average gestation length for mangabeys (Stabenfeldt and Hendrickx, 1973; Kinnaird, 1990). Females were classified as being in post-partum amenorrhea from the day of parturition until they developed the first sexual swelling post-partum. We excluded data collected from late March to early July 2010; a period when eight of nine cycling adult females and one adolescent female stopped cycling regularly and exhibited significantly different concentrations of fE and fP metabolites (Fernández, unpublished).

Fecal sample collection and hormone assays

To approximate the time of ovulation we collected fecal samples during Period 2 in order to determine the estrogen surge that precedes ovulation (Saltzman et al., 2010; Chapter 2). In total we analyzed 936 samples, including 735 from adult females (31.0 ± 19.8 samples/female; range: 3-71 samples) and 201 from adolescent females (67.0 ± 12.2 samples/female; range: 53-75 samples). On average, adult cycling females were sampled every 1.9 ± 0.9 days (range: 1-5 days) when they were approaching or were in MAX, and every 4.5 ± 2.1 days (range: 1-12 days) outside this period. Adolescent females were sampled on average every 2.3 ± 1.0 days (range: 1-8 days) for females approaching or in MAX, and every 5.2 ± 3.1 days (range: 1-20 days) for females outside this period. Fecal collection and preservation were conducted following Brockman and Whitten (1996). Briefly, recently deposited samples that had not been contaminated with urine were collected in Ziploc® bags containing a small silica gel package to initiate drying, and stored inside a thermos with an ice pack that had been cooled overnight in a mountain stream. Within two to eight hours, samples were dried in a Coleman® oven and stored in labeled Ziploc® bags with silica gel to absorb moisture, until shipped to the Smithsonian's National Zoological Park, Front Royal, VA, for analysis (Chapter 2).

Fecal extraction followed methods described in Velloso et al. (1998). Samples were lyophilized, sifted and stored in 5-ml polypropylene tubes until analyzed. Fecal extraction efficiency averaged 76.4 ± 15.2% based on recovery of radiolabeled steroid added to samples before extraction. Fecal estradiol and fP metabolites were quantified using enzyme immunoassay procedures (Chapter 2). Assay sensitivity was 40 pg/ml for fE and 50 pg/ml for the fP analysis. Inter-assay CVs of fE for low and high controls were 8.3% and 8.8%, respectively. For fP, inter-assay CVs were 5.5% for low and 10.5% for high controls.

Data analysis

Detection of Ovulation

We detected the estrogen surge that occurs prior to ovulation using methods described in Brown et al. (1996) and Chapter 2. We first calculated a baseline value of fE using an iterative process by excluding all values exceeding 1.5*SD above the mean (Brown et al., 1996). We then calculated the baseline using the remaining values. Next, we calculated the fE surge threshold, defined as 1.5 times above the aforementioned baseline (Brown et al., 1996; Chapter 2). Finally, we identified all fE peaks, that is, all fE values exceeding the fE surge threshold. As there were fluctuations in baseline fE (Chapter 2), only fE peaks that clearly rose higher than other fE values for that cycle were identified as estrogen surges. Whenever there were other fE values lower but of relatively similar to the fE highest peak, they were also considered part of the fE surge. We applied a similar method for the analysis of fP in order to identify the post-ovulatory progesterone rise that occurs after ovulation (Saltzman et al., 2010). Fecal progesterone levels, however, were uninformative in this regard, as they remained elevated throughout the menstrual cycle (Chapter 2), and thus could not be used for the detection of ovulation.

For the analysis of fE peaks we restricted our dataset to those cycles where hormonal samples were collected a minimum of 50% of days during MAX, the period when ovulation was most likely to occur (e.g., Aidara et al., 1981; Whitten and Russell, 1996; Emery and Whitten, 2003; Engelhardt et al., 2005; Brauch et al., 2007; Higham et al., 2008a; Daspre et al., 2009; Higham et al., 2012), to ensure the detection of the estrogen surge. When there were no samples the day before and/or after the fE surge, we included those days as part of the fE surge as well. In these cases, we considered the day with the observed fE peak, and the one or two days with missing data, as the potential estrogen surge. Thus, we were not able to narrow down the estrogen surge to a single day; rather, we defined an 'ovulatory window', which included the day(s) that fE rose above the fE surge threshold and was clearly higher than other fE values, plus the day(s) without samples on either side of it (Chapter 2). In the related *C. atys*, serum estradiol was metabolized and appeared in feces within 0 to 2 days (Whitten and Russell, 1996); therefore, we used a 24-hour time lag to account for metabolism (Whitten, pers. comm.). Ovulation, however, occurs 24 hours after serum estradiol peaks (Jeffcoate, 1983); thus, we use the day of the estrogen surge as the day fE exceeded the baseline in the feces (Higham et al., 2008b).

For adult females, we identified eight cycles that were well sampled during and around MAX, including four non-conceptive cycles that displayed the fE surge, three conceptive and one anovulatory cycle. One of these cycles occurred before September 2009; thus, the presence of the shiny phase was not coded. For adolescent females, we identified three ovulatory, non-conceptive cycles.

Changes in sexual swelling tumescence and appearance

To describe the changes in sexual swelling tumescence and appearance, we calculated the following parameters of non-conceptive cycles of adult females: 1) cycle length (from the first day of detumescence to the last day before the onset of the next detumescence); 2) inflation (from the first day the swelling starts to increase in size after reaching its minimum score, until the last day before reaching MAX); 3) MAX (the number of days the sexual swelling was at maximum size, i.e., score 5); 4) the shiny phase (the number of days during MAX with a shiny appearance); 5) deflation (from the first day of detumescence to the last day before the swelling reaches its minimum score); and 6) minimum swelling (from the first day after the end of deflation, i.e., the last day of detumescence, to the last day before the start of the next inflation, during which time the perineal skin in cycling females retained a small, constant turgidity). In five cycles, one day during the shiny phase was miscoded by the assistants as ‘shiny phase-absent’, while the following day the shiny phase was recorded as ‘present’. Given that such resumption of the shiny phase was not witnessed during any of the cycles coded by the project supervisor (DF), this was corrected and the shiny appearance was recorded as present for the entire time. We also determined whether the length of MAX correlated with the duration of the shiny phase. To do so we only used cases for which we knew the exact length of both. There were several menstrual cycles of adult females in which the sexual swelling deviated from the regular pattern of inflation – MAX – shiny phase – deflation (Table 3.2). We excluded all of these instances from the calculations of the characteristics of the sexual swellings and appearance (N = 8 cases).

Changes in sexual swelling tumescence and appearance in relation to ovulation

To investigate how changes in tumescence and appearance related to the timing the fE surge, for each cycle in which ovulation was detected, we plotted the periods of MAX aligned to the first day of detumescence. We used this to calculate the average number of days from the fE surge to the end of MAX.

Changes in maximum tumescence and appearance in relation to swelling type and female age

To determine if sexual swellings provide information to the male regarding the swelling type a female is undergoing and/or female age, we first analyzed differences in the duration of MAX and the shiny phase between non-conceptive and conceptive cycles of adult females. If the difference was not significant, we combined them and tested the value against the duration of swellings for females during different swelling types (first swelling post-partum after a surviving infant, first swelling after the death of an infant and post-conceptive swelling) and females in different age classes (adult vs. adolescent). If the difference was not significant, we tested the aforementioned swelling cycle types against swellings during conceptive and non-conceptive cycles separately.

Data treatment

To calculate the characteristics of the sexual swelling tumescence and appearance we limited our calculations to instances in which we knew the exact start and end day of each characteristic. To ensure that we did not bias our sample towards shorter durations, we also examined all cases when the exact start and end date were not known precisely, but could be determined to within 1 or 2 days. We report these values only when they fall outside the range of variation observed in the more precise data set. Prior to analysis, we screened data for equal variance, normal distribution and outliers. As our sample size was small, we used each measure (e.g., MAX duration), rather than each female, as the unit of analysis. Outliers were identified using the 'Outlier' function in SPSS 19.0 for Mac and were defined as values whose distance from the nearest quartile was greater than 1.5 times the interquartile range. Statistical analyses were conducted in R 2.15.2 (R-Development-Core-Team, 2012) for Mac. Differences in the duration of MAX and the shiny phase between sexual swelling types and between adult and adolescent females were assessed via Mann-Whitney U tests using the Coin package. All tests were two-tailed and evaluated with an alpha level of 0.05.

Results

Changes in the sexual swelling tumescence and appearance during the menstrual cycle

Cycle length in adult females, as defined by fluctuations in swelling tumescence, averaged 29.4 ± 1.6 days (range: 27-32 days, N = 8 cycles). Non-conceptive cycles of adult females included a mean period of inflation of 11.0 ± 5.2 days (range: 6-19, N = 5 cycles), a MAX period that averaged 6.5 ± 2.4 days (range: 5-8, N = 15 cycles) and a deflation period averaging 4.3 ± 1.3 days (range: 3-6, N = 4 cycles). Typically the sexual swelling did not deflate completely between the end of deflation and the start of inflation of the subsequent cycle. Rather a minimum swelling (score 8-1) was maintained for an average 8.8 ± 0.8 days (range: 8-10 days; N = 5 cycles; expanded sample size range = 2-15, N = 2 cycles). Adding up these components of the sexual swelling (i.e., inflation, MAX, deflation and minimum swelling) yielded a cycle length of 30.6 days, similar to the average cycle length reported above and within the range of observed cycles.

The average length of the shiny phase during non-conceptive cycles was 4.0 ± 1.7 days (range: 1-6, N = 11 swellings). In all known cases (N = 14 swellings: 11 known to the day plus three cases in which the shiny phase length was known to within 1-2 days), the MAX period was characterized by the shiny phase. The shiny phase began 3.0 ± 1.7 days (range: 1-6 days, N = 9 swellings) after the swelling reached MAX, and finished 1.0 ± 0.7 days (range: 0-2 days; N = 9 swellings) before the start of detumescence. We found a trend towards significance between MAX length and the duration of the shiny phase ($r_{(9)} = 0.334$, p = 0.063).

Timing of ovulation in relation to sexual swelling size and appearance

In all cases where fecal hormones and swelling data were available (N= 7 swellings), the fE surge occurred during MAX (Figure 3.1). In two cases (cycle ID: bad5 and bad1; Figure 3.1), the absence of hormonal samples on the first day of detumescence did not allow us to rule out the possibility that the surge occurred on the first day of detumescence. However, in no case did we observe a fE surge outside of MAX. On average, the ovulatory window occurred 3.7 ± 1.7 days (range: 0-6) before the start of detumescence (Figure 3.1). The first day of the shiny phase fell on the day of or the day preceding the fE surge in five of six cases, including three cycles in which conception occurred (cycle ID: kum2, ksr5, mdo3, kim1, mdo4; Figure 3.1).

Maximum tumescence and appearance of different swelling types and females of different age

Adult females during different swelling types

There was no significant difference in MAX duration for conceptive (7.3 ± 4.0 days) versus non-conceptive (6.9 ± 2.3 days) swellings (Mann-Whitney U: $z = 0.802$, p = 0.456; Table 3.3). We, therefore, combined non-conceptive and conceptive swellings and tested them against the other swelling types. Combined, the length of MAX averaged 7.1 ± 2.1 days.

Mean MAX duration of the first swelling post-partum after a surviving infant was 4.8 ± 2.4 days (N = 5 cases; range = 1- 7 days; extended sample yields one additional value of 8-10 days) (Table 3.3). When compared this to conceptive and non-conceptive cycles combined and found a trend towards significance (Mann-Whitney U: $z = 1.810$, p = 0.070), with a shorter MAX during the first swelling post-partum. We had only one case with accurate data of a female resuming cycling after the death of an infant, during which the female displayed MAX for 4 days. This was lower than the mean for swellings during conceptive and non-conceptive cycles combined but within the observed range.

During gestation, all females developed a single post-conceptive sexual swelling, which reached MAX 49.0 ± 1.4 days (range: 48-50 days, N = 3 post-conceptive swellings, extended dataset: 45-47 days) from the first day of detumescence of the conceptive cycle. One adult female displayed a swelling 55 days after the start of detumescence, but as it did not reach MAX, only swelling score 4, this case was excluded from the above calculation. The duration of MAX in post-conceptive swellings overlapped with that of cycling females (7.1 ± 2.1 days), and was not significantly different from MAX during conceptive and non-conceptive cycles (Mann-Whitney U: z = - 0.072, p = 0.967).

The shiny phase during conceptive cycles was shorter compared to non-conceptive cycles (1.7 ± 1.2 vs. 4.0 ± 1.7 days, respectively; Table 3.3), a difference that approached significance (Mann-Whitney U: z = -1.909, p = 0.070). To compare the shiny phase of other types of swellings, therefore, we will test them against the shiny phase of conceptive and non-conceptive swellings separately.

The first swelling post-partum after a surviving infant displayed a shiny phase that averaged 3.3 ± 1.5 days (range 1-7 days, N = 5 cases; extended dataset: 8-10 days N = 1 case) (Table 3.3). This mean was not significantly different than swellings during non-conceptive (4.0 ± 1.7 days; Mann-Whitney U: z = 0.716, p = 0.536) or conceptive (1.7 ± 1.2 days; Mann-Whitney U: z = -1.348, p = 0.300) cycles. The only observed case of a post-partum swelling after the death of an infant did not display a shiny phase. During post-conceptive swellings, only one of four females (25%) for which we have accurate data displayed a shiny phase, which lasted 6-7 days and was, therefore, longer than the average shiny phase of conceptive and non-conceptive swellings. The other females did not display the shiny phase at all (N = 2) or if they did, it lasted only one day (N = 1); however, as there was one day without data in each of these cases, we could not exclude the possibility that the shiny phase was displayed that day.

Adolescent females

Adolescent females developed a sexual swelling on average every 44.5 ± 8.5 days (range: 35-54, N = 4 cases; extended data set: 22-24 days N = 1) (Table 3.3), yielding a cycle length that was significantly longer compared to adults (Mann-Whiney U: $z = 2.732$, p = 0.002). Adolescents displayed MAX for an average of 8.9 ± 2.9 days (range: 5-12, N = 7 cases), which was not significantly different than MAX of adults females (Mann-Whiney U: $z = 1.289$, p = 0.210; Table 3.3). They also displayed the shiny phase in all swellings for which we have exact data (N = 9 swellings). The shiny phase averaged 6.4 ± 2.7 days (range: 3-11) (Table 3.3), which was significantly longer compared to both adult conceptive (Mann-Whiney U: $z = 2.403$, p = 0.012) and non-conceptive cycles (Mann-Whiney U: $z = 2.702$, p = 0.005).

Discussion

The mean menstrual cycle length for adult Sanje mangabeys was determined to be 29.4 ± 1.6 days, similar to the Sanje mangabey cycle length calculated between successive menses (30.0 ± 3.0 days: Chapter 2), and within the range of other *Cercocebus spp.* (34.0 days: Stabenfeldt and Hendrickx, 1973; 34.5 days: Hadidian and Bernstein, 1979; 30.8 days: Gordon et al., 1991; 27.5-30.1 days: Whitten and Russell, 1996; 31.0 days: Walker et al., 2004). MAX duration for adults was 6.5 ± 2.4 days, also within the range of other *Cercocebus spp.* (5-8 days: Whitten and Russell, 1996; 2-12 days: Walker et al., 2004), except that it is longer than values reported by Aidara and colleagues (1981) for a captive population of sooty mangabeys (2-3 days). During

MAX, sexual swellings became brighter (i.e., the shiny phase) for an average of 4.0 ± 1.7 days. The shiny phase has not been previously described for other *Cercocebus* spp. and thus there is no comparative reference value for this trait. It is possible that this trait is unique to the Sanje mangabey. More detailed studies on the sexual swellings of other *Cercocebus* mangabeys are necessary to elucidate the distribution of this trait.

In this study, fP levels remained highly variable during the menstrual cycle and could not be used for the detection of ovulation, for which we had to rely on the detection of fE surges (Chapter 2). Given the temporal and quantitative relationship that has been documented in *Cercocebus* mangabeys between fecal and serum estradiol, and between serum estradiol and the peri-ovulatory peak of follicle stimulating hormone (Aidara et al., 1981; Whitten and Russell, 1996), the fE surge should be a reliable proxy for ovulation (Chapter 2).

In all cases in which we had hormonal data, we found that the fE surge occurred during MAX, specifically towards the second half, 3.7 days before the onset of detumescence. This suggests that sexual swelling tumescence is a good indicator of female fertility. Additionally, we found that the shiny phase began the day preceding, or the day of, the fE surge in five of six cases, including the three cycles in which conception occurred. Therefore, the swelling appearance may more precisely indicate the timing of fertility than tumescence. Overall, these results suggest that in the Sanje mangabey sexual swellings may convey information to males about female fertility, signaling when it is more likely (during MAX, in particular during the shiny phase), but not its exact timing. This is in line with the graded signal hypothesis (Nunn, 1999), and parallels what has been reported for other mangabeys (Aidara et al., 1981; Whitten and Russell, 1996), as well for other primates with exaggerated sexual swellings in which ovulation also occurred during peak swelling (Wildt et al., 1977; Aidara et al., 1981; Shaikh et al., 1982; Reichert et al., 2002; Deschner et al., 2003; Emery and Whitten, 2003; Deschner et al., 2004; Engelhardt et al., 2005; Möhle et al., 2005; Brauch et al., 2007; Higham et al., 2008a; b; Daspre et al., 2009; Higham et al., 2012), particularly towards the end of MAX (Wildt et al., 1977; Shaikh et al., 1982; Reichert et al., 2002; Deschner et al., 2003; Engelhardt et al., 2005; Higham et al., 2008a; Daspre et al., 2009).

It seems, therefore, that in Sanje mangabeys sexual swellings prioritize paternity concentration over paternity confusion (Nunn, 1999; Zinner et al., 2002; Alberts and Fitzpatrick, 2012), as both tumescence and appearance contained information about female fertility. If this is the case, we would expect the alpha male to target and monopolize females towards the end of MAX, during the shiny phase. Nonetheless, although males display a dominance hierarchy and high ranked males guard females from subordinates (Chapter 4), female Sanje mangabeys have been observed mating promiscuously during MAX and the shiny phase, usually with more than one male per day (Chapter 4). Thus, despite the fertility signal the sexual swelling seems to contain, females may still be able to successfully confuse paternity among the males with which they mate.

That the appearance of the sexual swelling of Sanje mangabeys indicates the timing of the fE surge contrasts with what has been reported in other species, where coloration of the sexual skin was not found to provide information on the timing of ovulation (olive baboons: Higham et al., 2008b; rhesus macaques, *M. mulatta*: Dubuc et al., 2009). Our results are consistent, however, with a recent study on rhesus macaques that showed females' *facial* skin changed in luminance during the fertile phase (Higham et al., 2010). It is possible, that the 'appearance' of the sexual swelling in our study is not equivalent to the 'coloration' investigated in the former studies that used, for example digital images to measure the rate of red to green

(Dubuc et al., 2009) or a principal component analysis to collapse red, green and blue values into a color score (Higham et al., 2008b). Comparisons regarding the signal in the appearance of the sexual swelling of the Sanje mangabey and the coloration of the sexual swellings of other species, however, must be undertaken with caution, as they may not represent an equivalent signal.

We also compared the duration of MAX and the shiny phase among different types of sexual swellings to assess whether they could be used by males as clues to distinguish females undergoing different swelling types or females of a different age class. We found that MAX duration could potentially be used to identify the first swelling postpartum after a surviving infant and perhaps even after the death of an infant, as these swellings tended to be shorter. Similarly, we found that duration of the shiny phase could be used to distinguish conceptive swellings, which tended to have shorter shiny phases, from non-conceptive swellings, as well as the first swelling post-partum and the post-conceptive swelling, which were less likely to display the shiny phase at all. Adolescent females, on the other hand, displayed the shiny phase for longer compared to adult females. Taken together these results suggest that the sexual swelling of Sanje mangabeys can potentially provide information to male Sanje mangabeys on the timing of the fE surge, the likelihood that a cycle will be conceptive, and female age class. This would become particularly important during the conceptive season, from January through March when most conceptions occur (McCabe, 2012). If males are able to use sexual swellings to identify when females are most likely to ovulate, we can make predictions as to what females they would prefer when more than one female is receptive at a time. First, males should prioritize females that exhibit MAX, as this is when the fE surge is most likely to occur. In addition, among females at MAX, males should prefer to mate with those that have been at MAX for longer, as they are more likely to be in the second half of MAX, when the fE surge tends to occur. Finally, males should select females that display the shiny phase, because there is a higher probability of fE surging at this time, and the shiny phase is completed close to the end of MAX. Moreover, the shiny phase begins immediately before the fE surge, and during conceptive cycles females tended to displayed the shiny phase for shorter periods, suggesting that during conceptive cycles the fE surge occurs at the beginning of the shiny phase. In humans, sperm is viable for up to 3 days (Wilcox et al., 1995), and given that the ova is rarely viable for more than 24 h after its release (France, 1981), any copulation that occurs any time from 3 days prior to ovulation, to the day after ovulation, can potentially result in conception. As such, studies usually define a fertile window that encompasses the three days immediately before ovulation, the day of ovulation and up to three days after (e.g., Deschner et al., 2003; Harris and Monfort, 2006; Higham et al., 2009; Lu et al., 2012). Thus, to maximize the chances of fertilizing the ovum, males should prioritize females from the time immediately before through the time immediately after the start of the shiny phase.

The methods used in this study did not allow for the detection of small-scale changes over the course of one cycle in the tumescence of the sexual swelling, as has been found in some species (Deschner et al., 2004; Brauch et al., 2007; Higham et al., 2008b). These studies used photographic techniques to measure absolute sexual swelling size, which correlated with fE, and continued increasing even within the MAX period. These methods have also detected an increase in swelling size as a female underwent consecutive cycles (Emery and Whitten, 2003; Deschner et al., 2004; Higham et al., 2008b; Huchard et al., 2009), with the conceptive cycle displaying the largest sexual swelling (Alberts et al., 2006; Gesquiere et al., 2007; Daspre et al., 2009; Higham et al., 2012). If this also occurs in the Sanje mangabey, and males are able to identify small changes in size, they would have an additional morphological cue, other than the duration of MAX, to distinguish female reproductive state, or to pinpoint the time of ovulation (Deschner et al., 2004; Brauch et al., 2007; Higham et al., 2009). Given the accuracy of such a signal, we would expect males to guard females during ovulation, regardless of whether it occurs outside the shiny phase or outside MAX. An analysis of male sexual behavior and paternity testing will ultimately be required to accurately assess males' ability to detect the timing of ovulation. Once this has been established, we will be able to better understand the function of the sexual swelling in this species, and how that modulates female reproductive strategies by prioritizing paternity concentration or confusion (Alberts and Fitzpatrick, 2012).

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Figures and tables

Table 3.1. Description of the nine stages used to code sexual swelling tumescence in the Sanje mangabey. The scale was modified after Whitten and Russell (1996) and Walker et al. (2004).

Sexual swelling size change	**Sexual Swelling Score**	**Description**
Inflation	0	Sexual skin is completely flat
↓	1	Lower portion of the swelling, around the clitoris, starts inflating
	2	Circum-clitoral lobe becomes more prominent. First signs of tumescence around the labia
	3	Lower portion of the swelling is almost fully tumescent. Area around the anus, between the ischial callosities and the tail, starts to swell
	4	Lower portion is fully tumescent. Upper portion is mostly tumescent, except for two large wrinkles along each side
Maximum Tumescence*	5	The two wrinkles in the upper portion disappear and lower and upper portion are fully tumescent. Tail arches conspicuously at the base above the swelling
Deflation	6	Lower and upper portion of the swelling become wrinkly simultaneously, although the swelling remains largely tumescent. Sexual skin color becomes duller. Tail does not arch above swelling
↓	7	Turgidity is reduced considerable. Upper and lower portion becomes very wrinkly and acquire a dirty aspect
	8	Sexual skin is almost completely flat, but some folded skin is conspicuous

*The shiny phase occurs during size 5. See text for further details.

Table 3.2. Cycle anomalies observed and their presumed correlates for female Sanje mangabeys. None of these cycles were used in the calculations of the characteristics of the sexual swellings.

Cycle anomaly	Female ID	Duration (days)	Presumed correlate
Long inflation	mdo	93	Unknown
Long inflation	kum	60	Unknown
Does not reach MAX	mzu	n/a	First cycle after surviving infant
Does not reach MAX	yey	n/a	First cycle after death of 41-day old infant
Does not reach MAX	uvi	n/a	Second cycle after surviving infant
Long tumescence after MAX	bad	> 22	Returning to group after an absence of 31 days
No shiny phase	uvi	n/a	First cycle after surviving infant
No shiny phase	yey	n/a	First cycle after death of the infant

Table 3.3. Characteristics of maximum tumescence (MAX), shiny phase and swelling length [mean ± SD / (range) N] for different age-classes and sexual swelling types in the Sanje mangabey.

Age class	Sexual swelling type	Sexual swelling characteristic: MAX duration (days)	Sexual swelling characteristic: Shiny phase duration (days)	Cycle length (days)*
Adult	Cycling, non-conceptive	6.5 ± 2.4	4.0 ± 1.7	29.4 ± 1.6
		(5-8) 11	(1-6) 11	(27-32) 8
	Conceptive	7.3 ± 4.0	1.7 ± 1.2	-
		(3-11) 3	(1-3) 3	
	Post-conceptive	7.0 ± 1.4	0**	-
		(6-8) 2	(0) 2	
	1st swelling after PPA	4.8 ± 2.4	3.3 ± 1.5	-
		(1-7) 5	(2-5) 3	
	1st swelling after infant death	4	-	-
		(4) 1		
Adolescent	Cycling, non-conceptive	8.9 ± 2.9	7.0 ± 2.3	44.5 ± 8.5
		(5-12) 7	(3-11) 8	(34-54) 4

*Calculated from the end of MAX to the last day before the end of the next MAX period
**One case with known to within one day displayed the shiny phase for 6-7 days
PPA: post-partum amenorrhea

Figure 3.1. Pictures illustrating the sexual skin of female Sanje mangabeys (A) at score 0 or flat, (B) score 5 or maximum tumescence, (C) and score 6 or the beginning of detumescence. (D) Female displaying a sexual swelling in maximum tumescence.

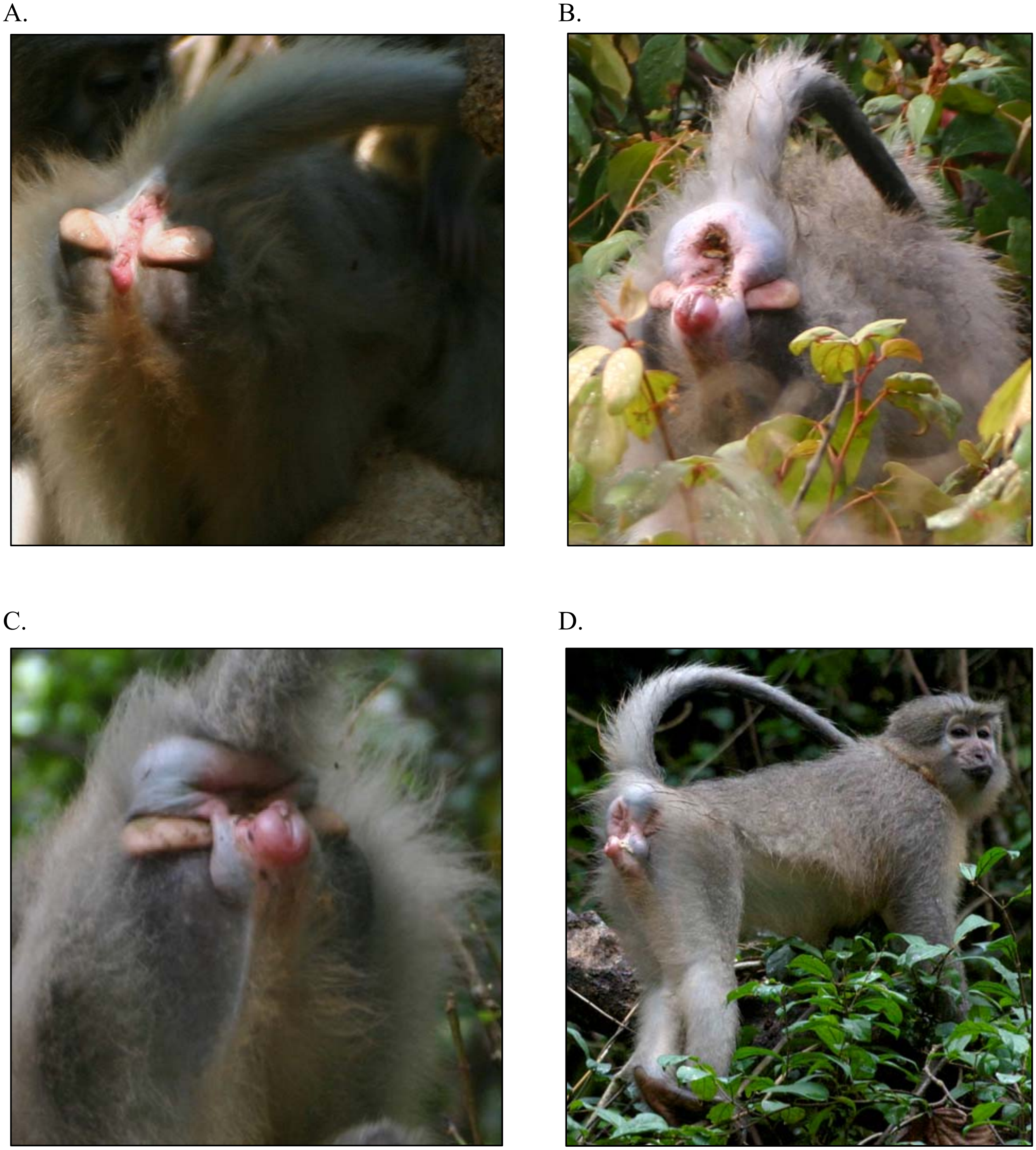
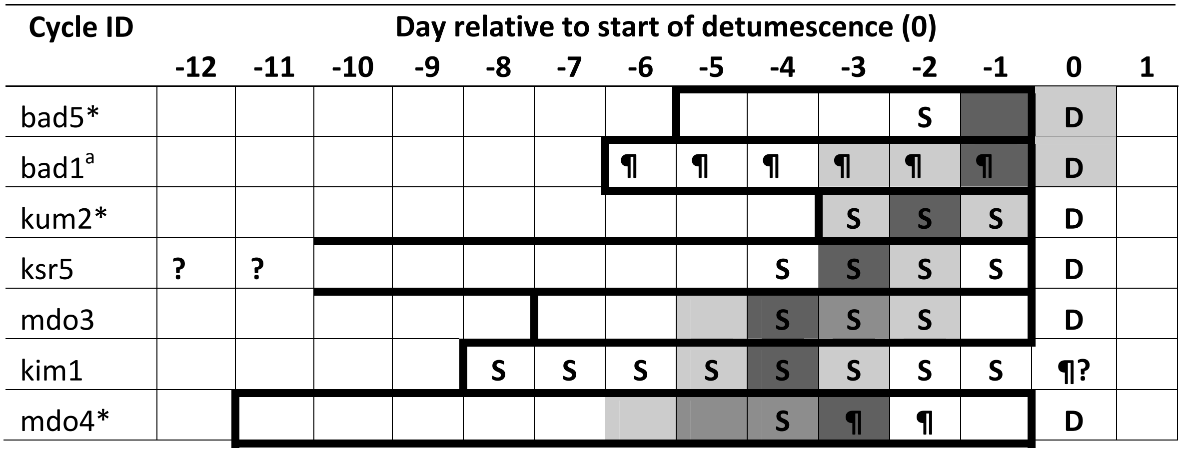


Figure 3.2. Maximum tumescence periods (bold outline) aligned with respect to the day of detumescence (day 0) for the Sanje mangabey. Grey-colored boxes indicate the days when ovulation could have occurred (the 'ovulatory window', see text for further details): Light grey boxes corresponds to days without fecal samples and thus without fecal estradiol (fE), medium grey to fE values lower by relatively similar to the fE surge; and dark grey to the highest fE value, indicative of the fE surge used as a proxy for ovulation. Cycles are ordered in terms of the proximity of the ovulatory window to the start of detumescence. 'S': the shiny phase. 'D': first day of detumescence. '?': unknown day of start of maximum tumescence or end of maximum tumescence. ¶No data on shiny appearance, '*': conceptive swelling.



Cycle ID	Day relative to start of detumescence (0)													
	-12	-11	-10	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	1
bad5*											S		D	
bad1[a]							¶	¶	¶	¶	¶	¶	D	
kum2*										S	S	S	D	
ksr5	?	?							S	S	S	S	D	
mdo3									S	S	S		D	
kim1					S	S	S	S	S	S	S	S	¶?	
mdo4*									S	¶	¶		D	

[a]Sexual swelling appearance (i.e., the shiny phase) was not recorded at the time this cycle occurred

CHAPTER FOUR:

MALE MATING BEHAVIOR IN RELATION TO OVULATION, SEXUAL SWELLINGS AND FEMALE FERTILITY IN SANJE MANGABEYS

To be submitted under the title 'Male mating behavior in relation to ovulation, sexual swellings and female fertility in Sanje mangabeys' by David Fernández

Abstract

In many primate species, male rank correlates with mating success. In such species, however, when two or more females are sexually receptive, the alpha male is unable to monopolize all females and concentrates his mating effort on the female that is closest to ovulation, giving subordinates the opportunity to gain access to females (priority of access model). When such reproductive synchrony occurs, males may also be able to distinguish among females of different reproductive quality, such as those exhibiting cycles that are more likely to be conceptive. Detecting ovulation, however, may be hindered in primates, particularly in species that display sexual swellings for an extended time, as females can mate throughout these prolonged periods, including outside the time of ovulation. Here I use behavioral observations of Sanje mangabeys (*Cercocebus sanjei*), a species in which females develop sexual swellings during menstrual cycles and pregnancy, to investigate whether males (N = 9) appear to show greater interest in females during the timing of ovulation (as determined by the analysis of fecal estradiol metabolites), and prefer swollen females of different fertility (menstrual non-conceptive, conceptive, post-conceptive) or female age (adults: N=18, adolescents: N=3). First, I examined how male mating skew varied in relation to female synchrony and found that males followed the priority of access model; thus, I limited the analysis of male interest to the behavior of alpha males. Alpha males displayed behaviors that imply greater interest in females during ovulation. They also preferred females during the shiny phase of their sexual swelling, a period during maximum tumescence in which the swelling acquired a brighter tone, which typically overlapped with ovulation; and particularly during the start of the shiny phase, which coincided with the highest fecal estradiol levels. Finally, they displayed greater interest in females undergoing what would become conceptive cycles compared to non-conceptive cycles, and less interest towards females displaying post-conceptive swellings, as well as in adult over adolescent females. Thus, male Sanje mangabeys appear to prefer females during ovulation, despite the long duration of the exaggerated sexual swellings and prolonged receptive periods of the females; however, paternity analysis will be necessary to verify that alpha males were successful at monopolizing females during the ovulatory period.

Keywords: *Cercocebus sanjei*, mate choice, priority of access, reproductive strategies, Udzungwa Mountains

Introduction

Male reproductive success is limited by access to fertile females (Trivers, 1972). In many primates living in multi-male groups, male reproductive skew is high, and rank determines access to females (Cowlishaw and Dunbar, 1991). In these species, when a single female is sexually receptive the alpha male is typically able to mate-guard the female, and thereby monopolize most copulations and sire most offspring (e.g., Dixson et al., 1993; de Ruiter et al., 1994; Altmann et al., 1996; Widdig et al., 2004; Brauch et al., 2008). When two or more females are sexually receptive at the same time (i.e., mating synchrony), however, the alpha male is no longer able to monopolize all available fertile females (Say et al., 2001; Takahashi, 2004; but see Setchell et al., 2005), and is predicted to concentrate mate-guarding and mating effort on the female that is most likely to conceive; i.e., closest to ovulation, provided the male is capable of detecting ovulation (Packer, 1979; Alberts et al., 1996; Wedell et al., 2002). This also provides the opportunity for subordinate males to achieve some mating success with females that are not targeted by the alpha (priority of access model, Altmann, 1962).

In many anthropoid primates, identifying when a female is ovulating is difficult because, rather than mating during the three day window surrounding ovulation when fertilization is most likely (France, 1981), as most mammals do (Heape, 1900), females also mate when conception is not possible, such as during non-fertile periods of the menstrual cycle through extended periods of receptivity (e.g., Bielert and Anderson, 1985; Aujard et al., 1998; Engelhardt et al., 2004; Carnegie et al., 2005; Stumpf and Boesch, 2005; reviewed in Dixson, 2012) and/or during gestation (e.g., Gust, 1994a; Soltis et al., 1999; Engelhardt et al., 2007; Doran-Sheehy et al., 2009; Fürtbauer et al., 2011; Lu et al., 2012). This decoupling of sexual behavior and fertility is particularly common in species where females advertise sexual receptivity with exaggerated sexual swellings (Dixson, 1983; reviewed in 2012), when periods of maximum swelling and mating may occur during as much as 73.5% of the menstrual cycle (bonobos, *Pan paniscus*: Dahl, 1986).

Sexual swellings are thought to function to both concentrate and confuse paternity, with ovulation typically occurring near the time of peak swelling, although with some uncertainty (graded signal hypothesis: Nunn, 1999). Accordingly male interest in females is also typically highest at peak swelling. For example, in experiments where artificial swellings were attached to ovariectomized (i.e., non-ovulating) female baboons, male sexual arousal significantly increased with increasing swelling size (Bielert and Anderson, 1985; Bielert and Girolami, 1986; Girolami and Bielert, 1987; Bielert et al., 1989; reviewed in Dixson, 2012). Given that high ranking males tend to monopolize females during peak swellings (e.g., chacma baboons, *Papio cynocephalus ursinus*: Bulger, 1993; mandrills, *Mandrillus sphinx*: Setchell et al., 2005; reviewed in Nunn, 1999), those that provide an accurate signal of female fertility would tend to allow females to concentrate paternity on the best male (presumably the alpha, the male with the highest competitive ability). For instance, studies that measured small-scale changes in the size of the sexual swelling, demonstrated that males had a preference for females at peak swelling (chimpanzees: Deschner et al., 2004; olive baboons: Higham et al., 2009), which coincided with the time of ovulation (Deschner et al., 2004; Higham et al., 2008b). Moreover, when examining male behavior towards maximally swollen females, in some species males showed an increase in their mating interest, as measured, for instance, by a higher copulation rate and longer consortships, around the time of ovulation (chimpanzees: Deschner et al., 2004; Barbary macaques: Heistermann et al., 2007; olive baboons: Higham et al., 2009; Sulawesi macaques: Daspre et al., 2009; Higham et al. 2012). Since subordinates usually gain some mating access outside the peak swelling period, when the probability of ovulation is lower but still higher than zero, exaggerated sexual swellings may also act to confuse paternity among these lower-ranked males. Less clear is whether males also prefer females during ovulation when it does not occur at peak swelling, although two studies have shown that males prefer ovulating females, even when ovulation does not occur at maximum swelling size (olive babons: Daspre et al., 2009; Sulawesi macaques: Higham et al., 2012), suggesting that they may use cues in addition to swelling size to choose females.

In species where mating synchrony occurs, males may display differential interest towards females based on female's reproductive quality. In several taxa, males prefer females that are undergoing conceptive versus non-conceptive cycles (savannah baboons: Bulger, 1993; Alberts et al., 2006; Gesquiere et al., 2007; chacma baboons: Weingrill et al., 2003; West African chimpanzees: Deschner et al., 2004; mandrills: Setchell et al., 2005). In mandrills, for example, alpha males consorted more with females during conceptive cycles compared to non-conceptive cycles (Setchell et al., 2005). Similarly, in some cases males appear to prefer cycling over pregnant females (but see Western gorillas, *Gorilla gorilla*: Doran-Sheehy et al., 2009). For example, alpha male sooty mangabeys limited mating to cycling females with sexual swelling versus pregnant females with post-conceptive swellings, which they also followed for significantly shorter periods and inspected less frequently (Gordon et al., 1991; Gust, 1994a). Similar results were found in Barbary macaques (Küster and Paul, 1984). Additionally, in most species males preferred the more fertile adults compared to adolescent females (reviewed in Bielert and Anderson, 1985), which undergo a period of adolescent sterility (Hartman, 1931; reviewed in Dixson, 2012). For instance, a study in baboons at Amboseli showed that males consorted more adult females than newly cycling adolescents (Gesquiere et al., 2007). Thus, when female synchrony occurs, being able to identify the female that has the highest reproductive potential could significantly increase the male's reproductive success.

In this study, I examine mate preference among male Sanje mangabeys (*Cercocebus sanjei*). This species is characterized by multi-male, multi-female groups (Ehardt et al., 2005), in which females exhibit exaggerated sexual swellings that remain at maximum tumescence (MAX) for an average of 7 days during a 30 day menstrual cycle (Chapter 2). Previously, I have shown that ovulation typically occurs during the last four days of MAX, just prior to detumescence

(Chapter 3). During MAX, Sanje mangabey females undergo approximately a four-day period in which the appearance of the sexual skin changes, acquiring a brighter tone, i.e., “the shiny phase”. This shiny phase coincides with ovulation, as it typically starts the day of, or the day prior to, the fecal estradiol (fE) surge, which is indicative of ovulation (Chapter 3), thus potentially acting as a further signal to males pinpointing female fertility. Females also exhibit a single post-conceptive swelling, during which they have been observed to mate with adult males (Fernández, unpublished). Additionally, the sexual swellings of females at different stages of fertility (cycling females in conceptive vs. non-conceptive cycles vs. pregnant females) and ages (adult vs. adolescent) differ in their tumescence and/or appearance (Chapter 3), which may provide males with cues to distinguish among females of different reproductive quality. Moreover, female Sanje mangabeys increase their urinary c-peptide levels, a measure of energy balance (i.e., energy intake minus expenditure, Emery Thompson and Wrangham, 2008), and their average fE levels as they undergo consecutive menstrual cycles, so that their urinary c-peptide and fE levels peak during conceptive cycles (McCabe, 2012).This may also convey additional information to males regarding the quality of the cycle.

I examine whether male Sanje mangabeys display behaviors that may indicate a greater interest towards females during ovulation and females of different reproductive quality. I do so by examining how male socio-sexual behavior (i.e., close proximity to females, approaches, anogenital inspections, mating solicitations, copulations, and rejections of female mating solicitations) differs towards females (1) during the time of ovulation compared to outside this period; (2) during different stages in the tumescence and appearance of the sexual swelling; and (3) for females of different fertility and age. As male dominance in Sanje mangabeys has not been described, I begin by examining whether males differ in rank, as they do in other closely related species (sooty mangabeys: Gust, 1994a; Range et al., 2007), and if female synchrony influences the relationship between male rank and mating success as predicted by the priority of access model (Altmann, 1962). In particular, I predict that mating skew will decrease as mating synchrony increases. To do so I first calculate female synchrony for days when the focal was at MAX and for days in which the focal displayed the shiny phase, as it is then that ovulation occurs, and thus it is expected that males will invest mating and guarding effort more heavily at this time (Bissonnette et al., 2011; Dubuc et al., 2011). Second, I calculate the expected mating skew based on female synchrony. Finally, to test the accuracy of the priority of access model I evaluate the observed male mating skew and how it compares to the expected value. If male Sanje mangabeys follow the priority of access model, I will assess male preference based solely on the behavior of the alpha male, since his behavior should be less constrained by other males due to his superior competitive ability.

If male Sanje mangabeys behave differently towards ovulating females, I predict they will prefer females during the time of ovulation compared to outside this period. In addition, as the shiny phase typically starts the day of, or the day prior to the fE surge, I predict that males will prefer females during the first two days of the shiny phase compared to the rest of the shiny phase. Similarly, males should prefer females during the shiny phase compared to during MAX outside the shiny phase, and females during MAX compared to other swelling stages. Finally, if males prefer females of higher reproductive quality, I predict that males will show greater interest towards cycling females during conceptive cycles compared to cycling females during non-conceptive cycles, cycling females compared to females with post-conceptive swellings, and adult versus adolescent females.

Methods

Study site and subjects

The study was conducted on one habituated group of Sanje mangabeys, the Mizimu group, in the Mwanihana Forest (7°40'–7°57'S, 36°46'–36°56'E) of the Udzungwa Mountains National Park, Tanzania. The habitat is a mosaic of montane and sub-montane tropical forest, with areas of deciduous primary and secondary forest (Lovett, 1993; Ehardt et al., 2005). The Mwanihana Forest receives an average annual rainfall of 1,750 mm (Lovett, 1996), with most (1,650mm) occurring during the rainy season from November to May. Sanje mangabeys exhibit a seasonal peak in conceptions (Jan. - Mar.: McCabe, 2012), although they can conceive and give birth throughout the year. During this study, eighteen infants were conceived during this peak period, while the remainder were conceived during Jul. 09 (N=2), Sep. 09 (N=1); Dec. 09 (N=1), Apr. 10 (N=1) and May 10 (N=1).

Sanje mangabeys exhibit female philopatry and male dispersal. The study group (Mizimu group) consisted of 63-65 individuals, including six to nine adult males, with three males immigrating into the group, 18 to 20 adult females, three adolescent females, and offspring. Adolescent females were distinguished from adults by their relatively larger and brighter sexual swellings, smaller body sizes, button-like nipples and light facial skin (Altmann et al., 1977; Sigg et al., 1982; Anderson and Bielert, 1994; Chapter 2). Individuals were identified using scars and facial skin coloration. In this study, I present data collected on 9 adult males, 18 adult females and 3 adolescent females.

Data collection

Data collection was divided into two periods: Period 1 (Oct. 13, 2008 - May 1, 2009) and Period 2 (Jun. 11, 2009 – Jul. 10, 2010). Typically the group was followed from sleep site to sleep site, an average of 8.8 ± 4.3 days per month during Period 1 (range: 4 – 18, total = 70 days), and 23.1 ± 6.0 days/month during Period 2 (range: 10 – 30 days, for a total of 3,346.4 sampling hours [10.36 ± 1.2 hours/observation day]; N = 338 days).

Data were collected by myself and five local field assistants: Clever P. Ngatwika (Oct. 13, 2008 - Apr. 5, 2010), Aly C. Mihambo (Oct. 13, 2008 – Nov. 13, 2009), Bakari S. Ponda (Mar. 14, 2009 – Jul. 10, 2010), Francis J. Masinde (Aug. 11, 2009 - May 8, 2010) and Aloyce M. Kigoma (Apr. 11, 2010 – Jul. 10, 2010). Inter-observer reliability tests on swelling score and behavioral data were conducted every four months to ensure consistency. A minimum agreement of 90% was required (Martin and Bateson, 2007).

During Period 1, each day during group follows, these data were recorded: 1) all demographic changes in the group (e.g., births, deaths, immigrations and disappearances); 2) sexual swelling score for each female, used to classify females into different reproductive states; 3) *ad libitum* sampling (Altmann, 1974) on all observed male-male agonistic interactions, including supplant, yield, aggression and chase (Appendix 1), which were used to construct the male dominance hierarchy. During Period 2, in addition to the aforementioned data, the team also collected 4) fecal samples from all females for ovarian hormonal analysis (see below), and 5) all day focal follows (Altmann, 1974) of a single female. Female focal follows began when a female was sexually receptive (typically swelling score 4; see Scoring sexual swelling tumescence) and continued until the end of her receptive period (usually the first day of detumescence or shortly thereafter). Once a focal had been selected, she was followed continuously for the duration of her receptive period, until she ceased mating with adult males (typically swelling score 6). At the end of the receptive period, a new focal was chosen randomly using the same criteria. Preference was given to females that had not been previously followed. I conducted a total of 24 focal follows of 14 different females (including 12 adult and 2 adolescents), that lasted an average of 7.4 ± 5.5 days, ranging from 1-21 days. In total there were 178 focal female days, of which the focal female was at MAX for 99 days and displayed the shiny phase for 49 days (Table 4.1). During focal follows, behavioral data on the socio-sexual behavior of the focal was collected, which was used to assess changing male interest in females.

Focal female behavioral data

Focal data were recorded using CyberTracker© version 3.129 (available at www.cybertracker.org) loaded onto a Palm© hand-held computer. During focal follows I continuously recorded all focal socio-sexual behavior (Appendix 1). This included all male socio-sexual behavior (and identity of male) directed towards the focal including: matings (and whether ejaculation occurred), approaches to within 5 meters, inspection of female anogenital area, mating solicitations, and female behavior directed towards the male including mating solicitation and the male's response (accept or reject) Additionally, at 15-minute intervals during the follows I noted the identity of all males within 5 meters of the focal.

Scoring sexual swelling tumescence and swelling appearance

Data on sexual swelling tumescence were collected using a 9-point scale (Chapter 3) (modified after: Whitten and Russell, 1996; Walker et al., 2004). Scores indicated: 1) the absence of any sexual swelling (score 0); 2) a sexual swelling increasing in tumescence (scores 1 to 4); 3) the MAX period, characterized by a completely turgid swelling (score 5); and 4) the period of detumescence (scores 6 to 8). Starting in September 2009, I also scored the sexual skin appearance *during* MAX, coding it as shiny or not shiny.

Female reproductive state

Female reproductive state was determined *a posteriori* based on fluctuations of the sexual swelling. Females were classified as cycling if they reached MAX *ca*. every 30 days, the average cycle length for other *Cercocebus* mangabeys (Hadidian and Bernstein, 1979; Whitten and Russell, 1996; Walker et al., 2004). The conceptive cycle was defined as the last swelling prior to the post-conceptive swelling, which reaches MAX approximately 50 days, rather than 30 days, after the previous swelling, (Hadidian and Bernstein, 1979; Kinnaird, 1990; Gust, 1994a; Walker et al., 2004). Conceptive and post-conceptive swellings were ultimately confirmed hormonally (Chapter 2) and/or with the birth of an infant.

Fecal sample collection, hormonal assays and interpretation

Methods of fecal sample collection and analysis have been described elsewhere (Chapter 2). Briefly, I analyzed 735 fecal samples from adult females (31.0 ± 19.8 samples/female; range: 3-71 samples) and 201 samples from adolescent females (67.0 ± 12.2 samples/female; range: 53-75 samples). Cycling adult females were sampled on average every 1.9 ± 0.9 days (range: 1-5 days) when they were approaching or in MAX, and every 4.5 ± 2.1 days (range: 1-12 days) outside this period. For adolescent females, samples were collected every 2.3 ± 1.0 days (range: 1-8 days) and 5.2 ± 3.1 days (range: 1-20 days), respectively. Samples were collected in Ziploc® bags containing a small silica gel package to initiate drying, and stored inside a thermos® with an ice pack that had been cooled overnight in a mountain stream, and dried in a Coleman® oven within two to eight hours after collection. Processed samples were stored with silica gel packages in a dark, cool place until shipped to the Smithsonian's National Zoological Park, Front Royal, VA (Chapter 2). Fecal extraction protocol followed Velloso et al. (1998; Chapter 2). Lyophilized samples were sifted and stored in 5-ml polypropylene tubes until assayed. Fecal extraction efficiency averaged 76.4 ± 15.2%. Fecal estradiol (fE) and progesterone (fP) were quantified using enzyme immunoassay procedures. Assay sensitivity was 40 pg/ml and 50 pg/ml for fE and fP, respectively; while inter-assay CVs for low and high controls for fE were 8.3% and 8.8%, respectively, and 5.5 and 10.5% for fP (see Chapter 2 for details).

To approximate the time of ovulation I detected the estrogen surge that occurs prior to ovulation through the analysis of fE metabolites (Brown et al., 1996; Chapter 2). Fecal progesterone was also analyzed but the values showed large fluctuations throughout the cycle, rendering it uninformative (Chapter 2). To detect the fE surge, I first calculated a fE baseline through an iterative process by which all fE values exceeding 1.5*SD above the mean were excluded (Brown et al., 1996). The baseline was calculated by averaging the remaining values. I used this baseline to calculate a fE surge threshold, defined as 1.5*baseline (Brown et al., 1996; Chapter 2). I then proceeded to identify all fE peaks indicative of the estrogen surge, defined as a fE value exceeding 1.5 times above the previously calculated baseline (Brown et al., 1996; Chapter 2). I only included cycles that were sampled at least 50% of the days of MAX, when ovulation was most likely to occur (e.g., Aidara et al., 1981; Whitten and Russell, 1996; Emery and Whitten, 2003; Engelhardt et al., 2005; Brauch et al., 2007; Higham et al., 2008a; Daspre et al., 2009; Higham et al., 2012). The fE surge was defined as a fE peak that clearly rose above other fE values for that cycle (Chapter 2). Neighboring fE values above the baseline that were of similar magnitude were considered part of the same fE surge (Chapter 2). Days immediately before and/or after a fE surge without fecal samples were also included as part of the peak, as I could not assume that fE had not been higher those days. As a result, in most cases I estimated an 'ovulatory window', which included the day(s) fE clearly peaked above the baseline, plus the day(s) without samples on either side of it. In *C. atys*, serum estradiol appears in feces between 0 to 2 days after being metabolized (Whitten and Russell, 1996); thus, I used a 24-hour time lag to account for hormonal metabolism (Whitten, pers. comm.). As ovulation occurs 24 hours after serum estradiol peaks (Jeffcoate, 1983), however, I used the day of the fE surge as the day of the estrogen surge (Higham et al., 2008b; Chapter 2). In total, I was able to determine the day of the fE surge in six follows (N = 69 focal days), including five from adult females and one from an adolescent female (Table 4.1).

Data analysis

Male dominance hierarchy

To calculate the male dominance hierarchy I analyzed all agonistic interactions (i.e., supplant, yield, aggression and chase) recorded during *ad libitum* sampling using the Elo-rating scores method (Albers and de Vries, 2001). Elo-rating is based on the sequence of interactions among individuals, rather than the interaction matrices commonly used to calculate dominance hierarchies (Albers and de Vries, 2001). At the start of the rating process, all individuals are assigned the same score. After each interaction, the rating of the winner increases, while the score of the loser decreases by the same amount. The exact amount of points gained and lost depends on the expectation of the outcome; that is, on the probability that the individual with the highest current score will win the next interaction (Elo, 1978). To establish a dominance hierarchy it is therefore not necessary that all individuals interact with each other. In addition, the Elo-rating procedure allows for demographic changes through time (e.g., migrations and immigrations), as individuals can be incorporated or removed from the hierarchy at any point (Neumann et al., 2011). Elo-ratings can also be used to monitor hierarchy dynamics and assess the stability of the hierarchy (Neumann et al., 2011).

Elo-ratings were calculated using a code written for R available from Neumann et al. (2011), with an initial score of 1,000 and a *k*-value of 100. The constant *k* determines the amount of points at stake during each interaction. In the short term, *k* influences the speed at which Elo-ratings change (e.g., higher *k*-values imply that more points are gained and lost after each interaction). For example, a male take-over would be reflected in the hierarchy faster with a relatively high *k*-value, and with some delay with a lower *k*-value, as the new dominant male would need to 'accumulate' enough of an Elo-score to surpass the deposed dominant male. Conversely, high *k*-values would also inflate the rate of rank turn-overs, thus the value selected should aim to accurately reflect the relationship among individuals. In the long-term, however, *k* has only a minor influence on the Elo-rating obtained (Neumann et al., 2011). I assigned the male with highest Elo-score as the alpha male, the male with the second highest as the beta, etc. The stability of the dominance hierarchy was assessed using the stability index *S*, defined as the ratio of rank changes per individuals present (Neumann et al., 2011). The *S*-index varies from 0 to 1, with 0 indicating a stable hierarchy and 1 a dominance hierarchy with high instability and constant rank turnovers (Neumann et al., 2011).

Priority of access model

To calculate the priority of access model I used data collected during female focal follows, excluding follows conducted on pregnant and adolescent females (N = 27 focal days), as these females may be less attractive than adult females undergoing menstrual cycles. I tested the model in two different ways. First, given that in Sanje mangabeys the ovulatory window is limited to the MAX period, I tested the model using only focal days in which the focal was at MAX (i.e., score 5, including shiny and non-shiny days; N = 82 days). In addition, because the ovulatory window is more likely to occur during the shiny phase, I also tested the model using a subset of data in which the focal displayed the shiny phase (i.e., score 5 during shiny days; N = 34 days) (Table 4.1).

Female synchrony and expected mating skew. To calculate MAX and shiny synchrony, I considered the subset of days when the focal was at MAX (N = 82) and shiny (N = 34 days), and calculated the number of other females that were simultaneously at MAX/shiny (Table 4.1). To calculate expected mating skew for days in which the female was MAX or shiny, each focal day I assigned an equal probability of mating (i.e., ejaculatory copulations) to each male whose rank was equal or lower than the total number of females at MAX/shiny. For example, on days when there was only one female at MAX, I assigned the alpha male a probability of 1 of mating with the female and a probability of 0 to all other males. When there were two females at MAX, I assigned a probability of 0.5 each to the alpha and beta male, and so on. I used a similar method to calculate synchrony of shiny days.

Observed mating skew. I calculated observed mating skew from the focal female's perspective. For each day the focal was at MAX and at shiny, I determined the proportion of focal female copulations with each male and averaged across the number of focal days examined in which the focal female was observed mating. Only ejaculatory copulations were included.

Testing the priority of access model. To test the model I first examined how the observed mating skew compared to the expected skew. Then, I evaluated if the observed mating skew deviated from a random distribution using the binomial skew index (B index: Nonacs, 2000; 2003). The B index tests the observed mating skew against a null hypothesis of random mating distribution ($B = 0$). A positive value indicates that the observed skew was greater than expected in compliance with the priority of access model, whereas negative values indicate that the mating skew was more equally distributed than expected. The B index was calculated using the Skew

Calculator 2003 (10,000 permutations), available online at https://www.eeb.ucla.edu/Faculty/Nonacs. Finally, I examined whether the observed mating skew during periods of overlap correlated with male rank using a Pearson correlation.

Male interest

Male behavior in relation to the ovulatory window. To assess whether males can detect the fE surge I examined if males behaved differently towards females during the ovulatory period, irrespective of swelling tumescence and appearance. In addition, because the ovulatory window tends to overlap with the shiny phase (Chapter 3) and therefore may be a confounding factor, as males may be cuing on the shiny phase rather than on the ovulatory window, I also examined if male behavior towards females that display the shiny phase varied compared to females that did not display the shiny phase. Therefore, this analysis only included follows for which I had ovulatory data available *and* during which I coded the appearance of the shiny phase (N = 4 follows, 41 focal days; Table 4.1). Each focal day was coded as occurring during (0) or outside (1) the ovulatory window and whether the focal displayed the shiny phase (0) or not (1). Overall, there were 9 focal days during the ovulatory window, 5 of which (55.6%) occurred during the shiny phase.

I used linear mixed models (model 1) to test whether males behaved preferentially towards females during versus outside the ovulatory window. In each model I tested whether one of the male behaviors (i.e., the response variable) differed relative to the ovulatory window (0/1) and swelling appearance (the presence/absence of the shiny phase (0/1), both included as predictor variables. The interaction between those two variables was also included as a predictor variable. Female ID and alpha male ID were incorporated into the model as random factors to account for females' and alpha males' unequal contribution to the dataset. Behavioral variables were not normally distributed even after log transformation, thus variables were treated as counts, and analyzed using generalized linear mixed models (GLMM) fitted with a Poisson error structure and a log link function. I included the (log-transformed) daily observation time (focal hours/day) as an offset variable, since that may have influenced the total number of times a behavior was observed on a given day; therefore, the response variables were treated as rates (Zuur et al., 2009). The exception was the proportion of times a male rejected a mating solicitation, which was offset by the number of mating solicitations received. As behaviors such as inspections and mating solicitations were rare, I converted those behaviors into 1-0 binary data to represent the daily presence (1) or absence (0) (e.g., Higham et al., 2009) and examined them using a GLMM with a binomial error structure and a logit link function. Model selection began with a full additive model; then, I sequentially removed non-significant predictor variables. The best model was ultimately chosen using the Akaike's information criterion (AIC) (Zuur et al., 2009).

Male behavior in relation to the start of the shiny phase. A second model (model 2) was created to examine if males displayed behaviors indicative of greater interest in females during the first two days of the shiny phase, which typically coincided with the fE surge, compared to the rest of the shiny phase. For this analysis, I included only focal days during the shiny phase (N = 49 focal days), regardless of whether or not hormonal data were available. The predictor variable included whether the follow was conducted on the first or second day of the shiny phase. The response variables, random factors and error distribution were similar to model 1.

Male behavior in relation to swelling score, cycle type and female age. A third model (model 3) was used to examine if males prefer females during MAX, and more precisely during the shiny phase, over other swelling scores, as well as females undergoing conceptive cycles over non-conceptive cycles and pregnant females, and adults over adolescent females, I examined male behavior in relation to these variables. For this analysis, I included all follow days for which I had scored the shiny phase, thus I excluded those days of MAX collected before September 2009 (N = 6 focal days; total sample size = 172 focal days). Model structure was similar as described above, with swelling score (score 4, score 5 [i.e., MAX excluding the days of the shiny phase], the shiny phase [i.e., MAX during the shiny phase] and swelling score 6), female age (adolescent, adult) and swelling type (menstrual-non-conceptive, conceptive, post-conceptive swelling) included as predictor variables, and one of the male socio-sexual behaviors as a response variable. All the predicator variables were defined as categorical, which means that I obtained a test statistic and a *p* value for all but the lower level of each variable (i.e., score 4, adolescent, and menstrual non-conceptive, respectively), which was by default considered the baseline and compared against each of the other levels (Zuur et al., 2009). Post-hoc comparison between score 5 and shiny were conducted by reordering the variable swelling score using the 'relevel' function, so that 'score 5' became the baseline value and thus the shiny phase level was compared against it. Post-hoc comparison of the proportion of solicitations ignored could not be compared using this method given the relatively low frequencies of this behavior, and thus it was conducted using Mann-Whitney U test.

All statistical analyses were conducted in R 2.15.2 (R-Development-Core-Team, 2012) using the lme4 package (GLMM) and the coin package (Mann-Whitney U test). In all GLMM models, assumptions for lack of over dispersion were met. All tests were two-tailed and considered statistically significant at $p < 0.05$.

<u>Results</u>

Male dominance hierarchy

Adult male Sanje mangabeys formed a clear dominance hierarchy (Figure 4.1). Overall, from Oct. 13, 2008 through Jul. 10, 2010, the dominance hierarchy showed a low S-index (S = 0.009) indicating that during the study male ranks were relatively unchanging. During the study period, however, there were two major changes. On Jan. 8, 2010, a male (usi) that was first seen with the group on Nov. 27, 2009, became the alpha-male, ousting the former alpha male (mas), who was absent from the group from Jan. 8 through 13, 2010. Given that the former alpha male had a relatively high Elo-score, and that changes in an individual's Elo-score are based on repeated interactions between individuals, this change in the hierarchy is not captured in the Elo-ratings until a few days later (Figure 4.1). The date of the take-over, however, is supported by the disappearance of the male 'mas', present on Jan. 7 but absent on Jan. 8, as well as on the interactions between 'mas' and the new alpha male upon the former's return to the group, which were won by the new alpha male 88.2% of the time (15 of 17 interactions).

The male take-over was followed shortly after by the immigration of a new male 'fat', that was first seen with the group on Jan. 28, 2010, and who acquired beta status on Feb. 9, 2010 (Figure 4.1). Accordingly, from the start of the study (Oct. 13, 2008) to the day prior to the male take-over (Jan. 7, 2010), the *S*-index was very low ($S = 0.005$). After the take-over, however, from Jan. 8, 2010, until the day 'fat' became the new beta male (Feb. 9, 2010), the S-index increased almost ten-fold ($S = 0.045$), reflecting the changes occurring in the dominance hierarchy. Finally, from the day after the new beta-male achieved his status (Feb 10, 2010) until the end of the study (July 10, 2010), the S-index decreased again ($S = 0.019$). Thus, for analysis of the priority of access model, I divided the study into three periods reflecting the identity of the alpha males and the stability of the hierarchy. These include: sub-period 1, from the start of the study (Oct. 13, 2008) until Jan. 7, 2010 (sub-period 1), during which time the male ‘mas’ was the alpha male; sub-period 2, from Jan. 8 through Feb. 8, 2010, from the day of the male take-over until the day the male ‘fat’ became the beta male; sub-period 3, from Feb. 9 until the end of the study (Jul. 10, 2001).

Priority of access model

To test whether male Sanje mangabeys follow the priority of access model, I used data collected during female focal follows, excluding days in which the focal was a) pregnant or b) an adolescent female. The model was tested independently for the subset of days in which the focal was at MAX (N = 82 focal days) and displayed the shiny phase (N = 34 focal days).

Female synchrony. Female synchrony was observed throughout the year, although, as expected, it was highest during the conceptive season, from January through March, which overlapped with male dominance sub-period 2, and with the first two months of sub-period 3. Out of the 82 days in which the focal females were at MAX, there was at least one other female at MAX on 74.4% of days (61 of 82). Similarly, out of the 34 focal days in which the focal displayed the shiny phase, the focal overlapped with at least one other female on 58.9% of days (20 of 34). Overall, during sub-period 1, there were an average of 1.7 ± 0.5 females at MAX per focal day (range: 1-2 females, N = 37 focal days), 2.8 ± 1.7 during sub-period 2 (range: 1-6 females, N = 14 focal days), and 3.4 ± 1.6 females per focal day during sub-period 3 (range: 1-6 females; N = 31 focal days) (Table 4.2). Synchrony of females with the shiny phase averaged 1.5 ± 0.5 females per focal day in sub-period 1 (range: 1-2 females, N = 11 focal days), 3.0 ± 1.9 females during sub-period 2 (range: 1-5 females, N = 5 focal days), and 2.7 ± 1.5 during sub-period 3 (range: 1-5 females; N = 18 focal days) (Table 4.2).

Observed mating skew. During days in which the focal female was at MAX, I observed 442 ejaculatory copulations (sub-period 1 = 186; sub-period 2 = 58; sub-period 3 = 198) distributed across 75 of the focal days (Table 4.2). This number does not include copulations in which the identity of the adult male was unknown (N = 3 ejaculatory copulations). There were 7 days in which the focal female was not observed mating. For days in which the focal displayed the shiny phase, 208 copulations were observed (sub-period 1 = 60; sub-period 2 = 22; sub-period 3 = 126) over 33 of the focal days (Table 4.2). The focal female was not observed mating during one day. Focal females typically mated with more than one male per day. On average, focal females at MAX mated with 2.3 ± 1.3 males per day (range: 0-6) during sub-period 1, with 2.1 ± 1.7 males during sub-period 2 (range: 0-5), and with 2.1 ± 1.7 males during sub-period 3 (range: 0-7) (Table 4.2). When the focal displayed the shiny phase, the average number of mating partners per day was 1.6 ± 0.8 males (range: 1-3), 2.4 ± 2.0 males (range: 0-5), and 2.2 ± 1.8 males (range: 1-7), during sub-period 1, 2 and 3, respectively.

There was a clear rank-based mating skew for copulations during focal days at MAX and during the shiny phase. The alpha male achieved 47.3% (88 of 186), 32.0 % (18 of 58) and 53.2% (100 of 198), of focal copulations when the focal female was at MAX during sub-periods 1, 2, and 3, respectively (Table 4.2). Similarly, when the focal displayed the shiny phase, the alpha male achieved 80.0% (48 of 60), 27.3% (6 of 22) and 52.7% (65 of 126) of copulations during sub-periods 1, 2 and 3, respectively (Table 4.2).

Testing the priority of access model. The observed proportion of focal female copulations by the alpha male closely matched predictions based on female mating synchrony, for sub-periods 1 and 3, for females at MAX and during the shiny phase, although it was less than expected during sub-period 2, the time of rank instability (Figure 4.2). Accordingly, during sub-periods 1 and 3, the observed mating skew across male ranks was relatively high and significantly different from a random distribution (sub-period 1: MAX focal day $B = 0.119$, $P < 0.001$; shiny focal days: $B = 0.472$, $P < 0.001$; sub-period 3: MAX focal day $B = 0.181$, $P < 0.001$; shiny focal days: $B = 0.204$, $P < 0.001$). The distribution of the data during sub-period 1, however, resulted in a non-significant correlation between observed mating skew and male rank given that only two females maximum were synchronous during this sub-period (MAX days: $r = -0.727$, $p = 0.102$, $N = 6$ males; shiny days: $r = -0.727$, $p = 0.109$, $N = 6$ males). While this situation facilitates alpha male monopolization of matings, it is not conducive to the statistical analysis of correlations. During sub-period 3, on the other hand, when female synchrony was higher than during sub-period 1, male rank significantly correlated with the observed proportion of copulations for shiny days ($r = -0.681$, $p < 0.05$, $N = 9$ males) and was close to significant for MAX days ($r = -0.650$, $p = 0.058$, $N = 9$ males), suggesting that during this period males of higher rank had an increasing advantage in gaining access to focal females over subordinate males.

In contrast, during the unstable sub-period 2, the distribution of copulations per male rank did not match the predictions of the priority of access model, with subordinate males accounting for a higher proportion of copulations than dominant males (Figure 4.2). This distribution of copulations still differs from a random distribution for MAX days ($B = 0.060$, $P < 0.001$), but not for shiny days, where it was close to being significant ($B = 0.041$, $P = 0.056$). Accordingly, the correlation between male rank and the proportion of ejaculatory copulations monopolized was not significant for MAX ($r = -0.358$, $p = 0.385$, $N = 8$ males) or the shiny phase, where the relationship was, in fact, positive ($r = 0.032$, $p = 0.946$, $N = 7$ males). This suggests that the significant and close to significant results of the B-index are driven by a relatively high proportion of matings by subordinate males, and not by what the priority of access model would predict. This is confirmed by the distribution of the proportion of matings by male rank (Figure 4.2). Thus, during sub-period 2, the observed skew does not follow the priority of access model, as high ranking males, particularly the alpha, monopolized a much smaller proportion of ejaculatory copulations compared to the other two sub-periods, while low ranking males successfully mated with the focal at a much higher proportion than expected (Table 4.2, Figure 4.2).

Alpha male interest

To examine male interest I used GLMM to analyze the effect on male behavior of a series of predictor variables, including the ovulatory window and the shiny phase (model 1), the first two days of the shiny phase (model 2), and swelling score, sexual swelling type and female age (model 3). The socio-sexual behaviors examined include: close proximity to females, approaches, anogenital inspections, mating solicitations, copulations, and rejections of female mating solicitations. Each analysis included one of the socio-sexual behaviors as the response variable. As male Sanje mangabeys followed the priority of access model, I limited the analysis to the behavior of alpha males.

Relationship between male behavior, the ovulatory window and the shiny phase

In this model I examined if the behavior of the alpha male towards females during the ovulatory window differed compared to outside the ovulatory window, as well as towards females during the shiny phase compared to outside the shiny phase. Thus, in this model I included the ovulatory window, the occurrence of shiny phase and their interaction as the predictor variables. The identity of the female and the alpha male were included as random factors. Behavior frequencies can be found in Table 4.3, while full model results are presented in Table 4.4.

Results indicate that alpha males preferred females during the ovulatory window versus outside the ovulatory window. During the ovulatory window, the alpha males increased the frequency at which they were found in close proximity ($z = -2.306$, $p < 0.05$), approached ($z = -4.016$, $p < 0.001$), and mated ($z = -2.190$, $p < 0.05$) with females, while rejecting a significantly lower proportion of female solicitations ($z = 3.660$, $p < 0.001$), compared to outside the ovulatory window (Table 4.4). No other behaviors of alpha males were affected by the ovulatory window (all $p > 0.1$). The appearance of the sexual swelling (i.e., the shiny phase) also had a significant effect on the approach rate ($z = 2.686$, $p < 0.001$) and the proportion of mating solicitations ignored ($z = 2.919$, $p < 0.01$) (Table 4.4); however, other behaviors were not affected ($p > 0.1$). In both cases, there was a significant interaction between the ovulatory window and the shiny phase (approach rate: $z = -3.594$, $p < 0.001$; proportion of solicitations ignored: $z = -4.352$, $p < 0.001$). A significant interaction can mean that there is no main effect of either of the predictor variables, or that the effect of one of the predictor variables depends on the levels of the other predictor variable. A visual examination of the frequencies of these two behaviors in relation to the ovulatory window and the shiny phase (Figure 4.3) revealed that the effect of shiny phase on the approach rate and the proportion of solicitations ignored disappeared when it did not overlap with the ovulatory window (Figure 4.3). This suggests that the shiny phase did not affect the behavior of the alpha male when controlling for the ovulatory window; thus, the alpha male showed greater interest in females during the ovulatory window, regardless of whether or not it coincided with the shiny phase.

Relationship between male behavior and the start of the shiny phase

Next, I examined if the socio-sexual behavior of the alpha males changed during the first two days of the shiny phase, which typically coincided with the fE surge, versus the rest of the shiny phase. This model included whether or not the follow had been conducted during the first two days of the shiny phase as the predictor variable, male behavior as the response variable, and the identity of the focal female and the alpha male as random factors. Behavioral frequencies and results of the statistical analysis can be found on Tables 4.5 and 4.6, respectively.

As predicted, results indicated that males appeared to show greater interest in females during the first two days of the shiny phase compared to the rest of the shiny phase. In particular, they were found in close proximity to the female for a greater proportion of time ($z = -2.383$, $p < 0.05$), and approached the focal female at a significantly higher rate ($z = -4.506$, $p < 0.001$) during the first two days of the shiny phase compared to later days within this phase. There was a trend, however, for the proportion of female mating solicitations ignored to decrease during the later days of the shiny phase compared to the first two days ($z = -1.652$, $p = 0.099$). There was no significant effect for other behaviors (all $p > 0.1$).

Relationship between male behavior, swelling score, cycle type and female age

Finally, I examined how the same socio-sexual behaviors varied in relation to a) the female swelling score (score 4, score 5 [i.e., MAX excluding the days of the shiny phase], the shiny phase [i.e., MAX during the shiny phase], score 6), b) to the swelling type the female is undergoing (menstrual conceptive, menstrual non-conceptive, post-conceptive), and c) to female age (adult, adolescent). To do so I used models that included these three variables as predictor variables, with each of the male behaviors, entered in turn, as response variables. The identities of the female and the alpha male were included as random factors. Behavior frequencies are presented in Table 4.7. Full model results can be found in Table 4.8.

a) Male behavior in relation to swelling score. As expected, all behaviors indicated that alpha males preferred females during swelling score 5 (i.e., MAX excluding the shiny phase] and especially during the shiny phase. More specifically, the rate at which alpha males were found in close proximity (score 5: $z = 5.141$, $p < 0.001$, shiny: $z = 9.672$, $p < 0.001$), approached ($z = 16.865$, $p < 0.001$; shiny: $z = 21.250$, $p < 0.001$) and mated with females (MAX: $z = 5.983$, $p < 0.001$, shiny: $z = 8.525$, $p < 0.001$), was significantly higher than during swelling 4, with the highest frequency of these behaviors during the shiny phase (Table 4.8). During the shiny phase, alpha males also decreased the proportion of mating solicitations ignored ($z = -4.479$, $p < 0.001$), and increased the probability that a male inspected ($z = 3.054$, $p = 0.002$) and solicited mating ($z = 2.096$, $p < 0.05$) compared to swelling 4. During score 5 there was a trend towards soliciting mating at a higher rate than during swelling 4 ($z = 1.814$, $p = 0.070$). Post-hoc comparisons revealed that compared to score 5 (i.e., MAX excluding the shiny phase), during the shiny phase alpha males significantly increased the rate at which they were found in proximity ($z = 6.197$, $p < 0.001$), approached ($z = 9.383$, $p < 0.001$), and mated with females ($z = 5.250$, $p < 0.001$), and exhibited a trend towards increased inspection of females ($z = 1.714$, $p < 0.087$). There were no differences in the proportion of solicitations rejected (Mann-Whitney U: $z = -1.0266$, $p = 0.3082$). Once females entered swelling score 6, which indicates the start of detumescence, alpha males decreased their interest, as the frequency at which they were found in close proximity to females significantly decreased compared to score 4 ($z = -2.423$, $p < 0.05$), and there was a trend toward rejecting more solicitations ($z = -2.195$, $p = 0.077$). All other behaviors were unaffected by the swelling score (all $p > 0.1$).

b) Male behavior in relation to swelling type. Results indicate that alpha males preferred females undergoing conceptive cycles over females undergoing non-conceptive cycles. In particular, alpha males significantly increased the rate at which they were found in close proximity ($z = 2.798$, $p < 0.01$) and approached females ($z = 2.730$, $p < 0.01$), and exhibited a significant decrease in the proportion of solicitations rejected ($z = - 3.818$, $p < 0.001$) (Table 4.8) during conceptive cycles. In contrast, alpha males were least interested in females with post-conceptive swellings, as they exhibited a trend towards decreasing the rate of being in close proximity and approaching females with post-conceptive swellings compared to those with swellings during non-conceptive cycles ($z = - 1.844$, $p = 0.07$; $z = - 1.996$, $p = 0.05$). None of the post-conceptive swellings included in the analysis, however, covered MAX or the shiny phase, as one of them did not reach MAX and on the other one data were collected before it did (Table 4.1), thus it cannot be ruled out that male the decreased interests shown toward pregnant females was driven by those swellings failing to reach MAX or the shiny phase, which is when males showed the most interest. Other behaviors were not significant (all $p > 0.1$).

c) Male behavior in relation to female age. Results showed that alpha males preferred adult over adolescent females, as they significantly increased the mating rate ($z = 2.470$, $p < 0.05$) and decreased the proportion of solicitations rejected ($z = -2.195$, $p < 0.05$) with adult females compared to adolescents. Alpha males also demonstrated a trend towards increasing their approach rate ($z = 1.702$, $p = 0.09$) to adults over adolescents (Table 4.8). Other alpha male behaviors were not affected ($p > 0.1$).

Discussion

This study investigated if male Sanje mangabeys exhibited a higher frequency of socio-sexual behaviors that may indicate male interest towards females during ovulation and towards females of different fertility. Given that male rank may influence access to females, I first examined male dominance relationships and if they followed a priority of access model (Altmann, 1962). Results demonstrated that males form a clear dominance hierarchy, with male rank determining access to females. Accordingly, the distribution of matings across males, particularly during days the focal displayed the shiny phase, was proportional to the male's rank, as predicted by the priority of access model. This pattern, however, broke down during the period of male rank instability, after the newly arrived male became the new alpha. During this time, two resident males, including the former alpha male, temporarily disappeared. This was followed by a period characterized by a high frequency of aggression in the group and one additional male immigrating and becoming the new beta male (Fernández and McCabe, unpublished). During this time, subordinate males had greater mating success compared to higher-ranked males. A similar case has been described in yellow baboons at Amboseli (Alberts et al., 2003), where periods of short male tenure, or periods when there was a relatively large number of males in the group, were accompanied by rank instability. During these times, the priority of access model was not in effect as males challenged each other for the top rank positions. Paternity analysis will ultimately confirm how successful alpha males were at monopolizing copulations and whether subordinates took advantage of the period of rank instability to increase their reproductive success.

It is also notable that the two males that ultimately became the alpha and beta joined the group in December 2009 and early February 2010, respectively, which was immediately before and soon after the start of the peak conceptive season (McCabe, 2012). This is similar to the male influxes that have been described for guenons and patas monkeys (Chism and Rowell, 1986; Cords, 1988; 2000), where extra group males join groups during the breeding season, at times even replacing the resident male (Enstam et al., 2002). Joining a group at this time of the year, when the number of receptive females peaks, would be a good strategy for solitary males. On the one hand, mature, young males at peak competitive ability could exponentially increase their reproductive success by becoming a top-ranking male. On the other hand, younger and older males that are not competitive enough for top positions could also enjoy greater mating opportunities during times of reproductive synchrony, particularly if the male hierarchy becomes unstable. There are no studies on the population structure or dispersal patterns of this species, but based on these results I predict that the number of solitary males would also be the highest during or immediately preceding the mating season, as has been found in species with male influxes (Cords, 2002).

One of the primary goals of this study was to determine if males could maximize the likelihood of paternity by increasing copulations during the most fertile period in the female's cycle. Results demonstrated that both alpha males appeared to show greater interest in females during the ovulatory window, at which time they were found in close proximity, approached and mated more frequently, and rejected fewer mating solicitations compared to outside the ovulatory window. These changes in behavior were independent of whether or not the ovulatory window overlapped with the shiny phase, which happened on 55.5% of the ovulatory window days (Chapter 3). Similar results were described in olive baboons and Sulawesi macaques (Daspre et al., 2009; Higham et al., 2012), where males showed greater interest in females during ovulation, even when it did not coincide with the largest size of the sexual swelling. It should be noted that the timing of ovulation could not be narrowed down to within 1 to 2 days, as has been possible in other studies in which males detected ovulation (e.g., Deschner et al., 2004; Heistermann et al., 2007; Daspre et al., 2009; Higham et al., 2009; 2012). Instead, the ovulatory window used in this study ranged from 2 to 4 days in length (Chapter 3). Thus, I cannot rule out the possibility that, rather than preferring females during the precise time of ovulation - the most fertile part of the cycle - male Sanje mangabeys prefer females during a 2 to 4 day time period that encompasses ovulation and the days around it.

When male behavior was examined in relation to the tumescence and appearance of the sexual swelling, independent of when the ovulatory window occurred, the frequency of the majority of socio-sexual behaviors analyzed also indicated that males appeared to show greater interest in females during the first two days of the shiny phase - which typically coincided with the fE surge - compared to later in the shiny phase, females at MAX outside the shiny phase, and to females during the period prior to, and after MAX. These results suggest that males may also use the shiny phase to identify females that are closer to ovulation.

The behavior of alpha male Sanje mangabeys indicates that they appeared to prefer females of higher fertility. They were in proximity, approached more often and rejected fewer mating solicitations from females undergoing conceptive vs. non-conceptive cycles. Further, males spent less time in proximity, approached less often and rejected more mating solicitations from females displaying post-conceptive swellings. It should be one of post-conceptive swellings included in the analysis did not reach MAX or the shiny phase (female ‘yey’, Table 4.1), while the other one the female was followed before it reached MAX (female ‘mdo’, Table 4.1). Thus, it may be the lack of these traits that signals that males target what might have been driving this decreased interest in post-conceptive swellings. Finally, alpha males preferred adult over adolescent females which was evident by an increase in the mating and approach rate, and a decrease in the proportion of solicitations rejected. Overall, these results parallel other studies in which the alpha males displayed more interest to females during ovulation, as well as to females undergoing cycles of different fertility, such as conceptive over non-conceptive swellings, and cycling over pregnant females (e.g., Bulger, 1993; Gust, 1994b; Weingrill et al., 2003; Gesquiere et al., 2007).

At this time, it remains unclear whether males were using behavior, physiology, olfaction or some additional cues as an ovulatory signal. For example, studies that have used digital photographs to measure absolute swelling size have found that swellings peaked in absolute size during ovulation (Deschner et al., 2004; Higham et al., 2008b), and males targeted females during that time (Deschner et al., 2004; Higham et al., 2009). Thus, in the Sanje mangabey it is possible that during the shiny phase, and potentially also during ovulation, the sexual swelling may be slightly larger than outside this period, and males may use this subtle increase in size as a cue for female fertility. Alternatively, in some species female proceptive behaviors (e.g., mating solicitations) are more frequently observed around the time of ovulation in conjunction with an increase in estradiol level (Wallen et al., 1984; Aujard et al., 1998; Carnegie et al., 2005; Engelhardt et al., 2005). Detailed analysis of female sexual behavior, including proceptive and receptive behavior during different swelling scores and the time of ovulation, would be necessary to determine whether males may be using female behavior to estimate female fertility.

More intriguing is males' greater interest in females undergoing a conceptive cycle compared to non-conceptive cycles. It is possible that the behavioral differences males displayed may have been unrelated to the female's attractivity and instead was a consequence of the number of receptive females (reproductive synchrony) during the time of ovulation. More specifically, a high number of receptive females may lead to a decrease in the alpha male's behaviors that indicate interest (e.g., mating frequency), as he may try to mate with several females, rather than focus his mating effort on the focal female. This may have caused a reduction in the sperm available and therefore, a reduction in the probability of conception

(Small, 1988). However, the maximum observed number of females displaying the shiny phase - when ovulation is most likely - was 5, and the number of adult males available ranged from 6 through 9. Thus, it is unlikely that the difference between conceptive and non-conceptive cycles was the result of the availability of sperm, as there were more adult males available than synchronous females. Instead, the difference may be due to female physiology during conceptive cycles. As previously mentioned, female Sanje mangabeys increase their average urinary c-peptide (i.e., their energy balance) and fE levels as they undergo consecutive cycles, with the highest levels recorded during conceptive cycles (McCabe, 2012). During the study most conceptions occurred from February to May, well into the period of high food availability - which lasts from November through May - after females have experienced several consecutive months of steady increase in energy balance and fE (McCabe, 2012). The two conceptive cycles included in the behavioral analysis also occurred during the high food period (female ‘bad’: December 2009; female ‘ksk’: February 2010. Table 4.1). It is possible, therefore, that males are able to cue on a change in odor that indicates when a female is experiencing high levels of urinary C-peptide and/or fE, and thus, is more likely to conceive during a particular cycle. This is supported by a study in chacma baboons (Weingrill et al., 2003), in which group males that had been resident for longer consorted females during conceptive cycles, while newly-arrived males of high rank consorted more often with females during non-conceptive cycles, suggesting that the assessment of conceptive over non-conceptive cycles improves with familiarity. While catarrhine primates have lost the vomeronasal organ, a chemical-sensing organ (Maier, 2000) found in strepsirhines, tarsiers and several platyrrhine taxa (reviewed in Smith et al., 2001), there is evidence that olfaction still plays a role in catarrhine primate reproduction, including that of humans (Keverne, 2004; Cerda-Molina et al., 2006; Clarke et al., 2009a; Haselton and

Gildersleeve, 2011; Gildersleeve et al., 2012). Alternatively, males may have cued on increases in absolute swelling size relative to a female's previous swellings, as in some species, sexual swellings become larger as females undergo consecutive cycles (Emery and Whitten, 2003; Deschner et al., 2004; Higham et al., 2008b; Huchard et al., 2009), with the conceptive cycle displaying the largest swelling (Alberts et al., 2006; Gesquiere et al., 2007; Daspre et al., 2009; Higham et al., 2012). A measure of absolute swelling size, rather than the scale used in this study, which measured relative changes in the swelling tumescence, will be necessary to examine if the sexual swelling of Sanje mangabeys are largest during conceptive cycles.

In this study, I demonstrated that females were guarded and mated more often with dominant males during their most fertile period. Alpha males, however, did not monopolize all copulations during the shiny phase, which illustrates that despite mate-guarding and possible sexual coercion, given that females have a smaller body size compared to males (Smuts and Smuts, 1993), females were able to mate promiscuously with both dominant and subordinate males during their receptive period. These results are in line with the graded-signal hypothesis (Nunn, 1999), which argues that sexual swellings function both to concentrate paternity in the best male (i.e., those with the highest competitive ability), and confuse paternity among other males. This strategy allows females to gain reproductive benefits, by conceiving with the best male, while obtaining additional paternal support for their infants and themselves from subordinate males (Taub, 1980; Hrdy, 1981; van Noordwijk, 1985; Harvey and May, 1989; Palombit et al., 1997; Borries et al., 1999). Whether subordinate males were more likely to support females and their infants after mating when conception was less likely is yet to be examined, although such an analysis would reveal the ultimate benefits of this strategy for females.

It is not yet known whether female behavior influenced alpha male reproductive success. In other species with large sexual dimorphism and/or where males guard mating partners, females can use the graded nature of the sexual swelling and prolonged receptive period to successfully implement the aforementioned reproductive strategy of paternity concentration and confusion. They may do so by being more selective, targeting males of higher rank during the peri-ovulatory period, and less so outside the peri-ovulatory period (Stumpf and Boesch, 2005; Barelli et al., 2008; Knott et al., 2010; Lu et al., 2012; but see Possamai et al., 2007) as well as during gestation (Gordon et al., 1991; Carnegie et al., 2005; Engelhardt et al., 2007; Clarke et al., 2009b). Female Sanje mangabeys regularly both solicited and rejected matings from other males when the guarding male was distracted; therefore, it is possible that these females were able to implement their own reproductive strategies. Whether females actually target males of higher rank (reviewed in Manson, 2007), or if they prefer males based on other characteristics, such as those with whom they have a higher gene compatibility (Schwensow et al., 2008), or males recently immigrated into the group (Boinski, 1987), remains to be investigated.

In summary, this study has demonstrated that male Sanje mangabeys follow the priority of access model, where rank determines access to fertile females. As such, alpha males displayed an increase in behaviors indicative of greater interest in females when they were more likely to ovulate (i.e., during the start of the shiny phase) and more specifically during the time of the fE surge. Alpha males were found to be capable of assessing female fertility, as they preferred females undergoing conceptive over non-conceptive cycles, as well as adults over adolescent females. Results showed that males displayed the least interest in females with a post-conceptive swelling, although this may have been related to post-conceptive swellings included in the analysis, which did not cover MAX or the shiny phase. These results provide further support for the graded-signal hypothesis; i.e., that exaggerated sexual swellings in primates may have evolved to allow females to both concentrate and confuse paternity, thereby increasing their reproductive success. Ultimately, paternity analysis will be necessary to accurately assess the success of alpha male reproductive strategies and their ability to estimate the timing of ovulation and monopolize females at this time.

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Figures and tables

Table 4.1. Summary of focal follows conducted indicating the duration, whether hormonal data were available, the number of days during the follow in which the focal was at maximum tumescence (MAX), swelling score 5 (i.e., maximum tumescence excluding the shiny phase) and displaying the shiny phase, the number of days of MAX and shiny synchrony (i.e., days in which there were other females at MAX and shiny phase, respectively, at the same time as the focal female), the type of sexual swelling, and the age of the focal. Follows are ordered first by the availability of hormonal data, then by swelling type and lastly by age class.

Female ID	Follow duration (days)	Hormonal data available?	Swelling type	Age class	# days focal at MAX	# days focal at score 5	# days focal at shiny	# days of MAX synchrony	# of days of shiny synchrony
bad	4	Yes	Cycling, conceptive	Adult	4	3	1	0	0
bad	21	Yes	Cycling, non-conceptive	Adult	6	6	Unk[1]	4	0
mdo	14	Yes	Cycling, non-conceptive	Adult	7	4	3	6	3
mbi	10	Yes	Cycling, non-conceptive	Adult	7	2	5	7	5
ksr	14	Yes	Cycling, non-conceptive	Adult	10	6	4	10	5
kad	5	Yes	Cycling, non-conceptive	Adolescent	3	0	3	2	0
ksk	6	No	Cycling, conceptive	Adult	5	5	0	4	0
ksk	5	No	Cycling, non-conceptive	Adult	0[*]	0[*]	0[*]	0[*]	0[*]
yey	5	No	Cycling, non-conceptive	Adult	0[*]	0[*]	0[*]	0[*]	0[*]
ham	5	No	Cycling, non-conceptive	Adult	4	1	3	0	0
ksk	1	No	Cycling, non-conceptive	Adult	0	0	0	0	0
ksr	5	No	Cycling, non-conceptive	Adult	3	2	1	0	0
mad	3	No	Cycling, non-conceptive	Adult	0	0	0	0	0
kab	5	No	Cycling, non-conceptive	Adult	1	1	0	1	0
kum	12	No	Cycling, non-conceptive	Adult	6	4	2	3	0
mdo	3	No	Cycling, non-conceptive	Adult	3	2	1	3	1
bad	4	No	Cycling, non-conceptive	Adult	4	4	0	4	0
ksr	15	No	Cycling, non-conceptive	Adult	10	5	5	4	0
kim	11	No	Cycling, non-conceptive	Adult	5	1	4	5	4
mos	8	No	Cycling, non-conceptive	Adult	7	2	5	7	2
kad	3	No	Cycling, non-conceptive	Adolescent	2	1	1	0	1
ten	16	No	Cycling, non-conceptive	Adolescent	12	1	11	10	5
yey	1	No	Pregnant	Adult	0[*]	0[*]	0[*]	0[*]	0[*]
mdo	2	No	Pregnant	Adult	0	0	0	0	0

[1] Follow was conducted before the shiny phase started being coded

[*] The sexual swelling did not reach maximum tumescence

Table 4.2. Number of days per sub-period in which there were ≥ 1 females in maximum tumescence (MAX) and displaying the shiny phase, used to estimate female synchrony; and number and proportion of ejaculatory copulations observed per male, a measure of mating skew. To test the priority of access model I divided the period of behavioral data collection into three sub-periods corresponding to the different identities of the alpha male and the relative stability of the hierarchy. Female synchrony was used to calculate the expected male mating skew and compared against the observed proportion of ejaculatory copulations.

Sub-period	**N days with females at MAX/shiny**						**Number of ejaculatory copulations per male rank on MAX/shiny days**									**Proportion of ejaculatory copulations per male rank on MAX/shiny days**								
	Number of females						**Male rank**									**Male rank**								
	1	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	12/6	25/5	0/0	0/0	0/0	0/0	88/48	28/5	19/3	24/1	10/3	17/0	N/A	N/A	N/A	0.47/0.75	0.13/0.09	0.11/0.06	0.12/0.03	0.06/0.07	0.10/0.00	N/A	N/A	N/A
2	4/2	3/0	3/0	1/2	2/1	1/0	18/6	0/0	4/2	8/2	14/0	14/6	0/6	0/NA[*]	N/A	0.32/0.23	0.00/0.00	0.07/0.09	0.11/0.09	0.26/0.37	0.22/0.23	0.00/0.00	0.00/N/A[*]	N/A
3	5/6	5/3	3/2	9/5	7/2	2/0	100/65	31/23	11/11	0/0	22/7	12/7	13/8	5/2	4/3	0.53/0.53	0.16/0.18	0.04/0.07	0.00/0.00	0.09/0.06	0.06/0.05	0.07/0.07	0.02/0.02	0.02/0.02

[*] Male joined the group after the last day of sub-period 2 when there synchronous females in the shiny phase

Table 4.3. Mean values of male behavior relative to the ovulatory window and the appearance of the sexual swelling (i.e., the shiny phase). Values were calculated including only follows for which ovulatory data were available and that were collected after September 2009, when I began coding the appearance of the sexual swelling. For rate behaviors, values represent N/hour. For binary variables, values represent the proportion of focal days in which the behavior occurred.

Male rank	Behavior	Quantification	Ovulatory window		Appearance	
			Ovulation	No-ovulation	Shiny	No-shiny
Alpha	Found in proximity	Count offset for observation time (i.e., rate)	0.40	0.18	0.29	0.25
	Approach	Count offset for observation time (i.e., rate)	5.35	2.42	3.62	3.51
	Mate	Count offset for observation time (i.e., rate)	0.41	0.31	0.39	0.33
	Ignore female solicitation	Count offset for solicitations received (i.e., proportion)	0.90	0.91	0.88	0.92
	Male solicitation	Binary (male does or does not)	0.00	0.26	0.10	0.25
	Male inspection	Binary (male does or does not)	0.55	0.47	0.50	0.50

Table 4.4. Results of the generalized linear mixed models that examined the behavior of the alpha male in relation to the ovulatory window and the appearance (i.e., the shiny phase) of the sexual swelling.

Male behavior	Predictor	Estimate	SE	*z*	*p*
Found in proximity	Ovulation	**-0.607**	**0.263**	**-2.306**	**p < 0.01**
	Appearance	0.215	0.173	1.242	n.s.
	Ovulation*appearance	**-0.759**	**0.304**	**-2.494**	**p < 0.05**
Approach	Ovulation	**-0.671**	**0.167**	**-4.016**	**p < 0.001**
	Appearance	**0.261**	**0.097**	**2.686**	**p < 0.01**
	Ovulation*appearance	**-0.666**	**0.185**	**-3.594**	**p < 0.001**
Mate	Ovulation	**-0.641**	**0.293**	**-2.190**	**p < 0.05**
	Appearance	-0.425	0.285	-1.492	n.s.
	Ovulation*appearance	-0.416	0.540	-0.770	n.s.
Ignore female solicitation	Ovulation	**1.652**	**0.451**	**3.660**	**p < 0.01**
	Appearance	**2.566**	**0.879**	**2.919**	**p < 0.01**
	Ovulation*appearance	**-5.059**	**1.163**	**-4.352**	**p < 0.001**
Solicit mating	Ovulation	17.140	4340.350	0.004	n.s.
	Appearance	1.464	1.129	0.000	n.s.
	Ovulation*appearance	-5.915	1.129	0.000	n.s.
Inspect	Ovulation	-0.873	0.856	-1.020	n.s.
	Appearance	0.111	0.880	0.126	n.s.
	Ovulation*appearance	0.862	1.832	0.470	n.s.

Table 4.5. Mean values of alpha male behavior during the first two days of the shiny phase and the days after (days 3rd to 11th). For rate behaviors, values represent N/hour. For binary variables, values represent the proportion of focal days in which the behavior occurred.

Male rank	Behavior	Quantification	Days of shiny phase	
			1 & 2	After day 2
Alpha	Found in proximity	Count offset for observation time (i.e., rate)	0.27	0.19
	Approach	Count offset for observation time (i.e., rate)	3.11	1.91
	Mate	Count offset for observation time (i.e., rate)	0.42	0.37
	Ignore female solicitation	Count offset for solicitations received (i.e., proportion)	0.58	0.63
	Male solicitation	Binary (male does or does not)	0.14	0.07
	Male inspection	Binary (male does or does not)	0.59	0.63

Table 4.6. Results of the generalized linear mixed models that examined the behavior of the alpha male during the first two days of the shiny phase compared to the rest of the shiny phase (days 3rd to 11th).

Male behavior	Estimate	SE	*z*	*p*
Found in proximity	**-0.265**	**0.111**	**-2.383**	**$p < 0.05$**
Approach	**-0.305**	**0.068**	**-4.506**	**$p < 0.001$**
Mate	0.022	0.168	0.128	n.s.
Ignore female solicitation	-1.305	0.790	-1.652	$p = 0.01$
Solicit mating	-0.800	1.082	-0.740	n.s.
Inspect	0.206	0.701	0.294	n.s.

Table 4.7. Mean values of alpha male behavior for three predictor variables: swelling score (score 4, score 5 [i.e., MAX excluding the days of the shiny phase], the shiny phase and score 6), swelling type (menstrual-non-conceptive, conceptive, post-conceptive swelling) and female age-class (adult, adolescent). For rate behaviors, values represent N/hour. For binary variables, values represent the proportion of focal days in which the behavior occurred.

Male rank	Behavior	Quantification	Swelling score				Swelling type			Female age	
			4	5*	Shiny	6	Non-conceptive	Conceptive	Post-conceptive	Adult	Adolescent
Alpha	Found in proximity	Count offset for observation time (i.e., rate)	0.10	0.18	0.22	0.04	0.14	0.34	0.05	0.16	0.07
	Approach	Count offset for observation time (i.e., rate)	0.60	2.27	2.45	0.31	1.34	4.27	0.04	1.70	0.37
	Mate	Count offset for observation time (i.e., rate)	0.07	0.29	0.39	0.04	0.19	0.53	0.14	0.24	0.04
	Ignore female solicitation	Count offset for solicitations received (i.e., proportion)	0.67	0.52	0.60	0.77	0.64	0.17	N/A	0.53	0.90
	Solicit mating	Binary (male does or does not)	0.02	0.11	0.10	0.05	0.08	0.00	0.00	0.08	0.00
	Inspect	Binary (male does or does not)	0.31	0.43	0.61	0.33	0.43	0.50	0.30	0.42	0.50

*Maximum tumescence excluding days with the shiny phase

Table 4.8. Results of the generalized linear mixed models that examined the behavior of the alpha male in relation to: swelling score (score 4, score 5 [i.e., MAX excluding the days of the shiny phase], the shiny phase [i.e., MAX during the shiny phase], score 6), the swelling type the female is undergoing (menstrual conceptive, menstrual non-conceptive, post-conceptive), and female age (adult, adolescent).

Male behavior	Predictor	Level	Estimate	SE	z	p
Found in proximity	Sexual swelling score	Score 5, no shiny	**0.660**	**0.130**	**5.081**	**$p < 0.001$**
		Shiny phase	**1.230**	**0.128**	**9.618**	**$p < 0.001$**
		Score 6	**-0.514**	**0.209**	**-2.456**	**$p < 0.05$**
	Swelling type	Conceptive	**0.392**	**0.140**	**2.798**	**$p < 0.01$**
		Post-conceptive	-1.096	0.595	-1.844	$p = 0.07$
	Female age	Adult	0.654	0.760	0.860	n.s.
Approach	Sexual swelling score	Score 5, no shiny	**1.844**	**0.109**	**16.865**	**$p < 0.001$**
		Shiny phase	**2.346**	**0.110**	**21.250**	**$p < 0.001$**
		Score 6	0.275	0.166	1.657	$p = 0.01$
	Swelling type	Conceptive	**0.232**	**0.085**	**2.730**	**$p < 0.01$**
		Post-conceptive	**-2.012**	**1.008**	**-1.996**	**$p < 0.05$**
	Female age	Adult	1.665	0.978	1.702	$p = 0.09$
Mate	Sexual swelling score	Score 5, no shiny	**1.812**	**0.257**	**7.065**	**$p < 0.001$**
		Shiny phase	**2.590**	**0.270**	**9.611**	**$p < 0.001$**
		Score 6	0.324	0.425	0.761	n.s.
	Swelling type	Conceptive	0.081	0.284	0.283	n.s.
		Post-conceptive	1.141	0.810	1.408	n.s.
	Female age	Adult	**2.755**	**1.101**	**2.502**	**$p < 0.05$**
Ignore female solicitation	Sexual swelling score	Score 5, no shiny	-0.009	0.666	-0.014	n.s.
		Shiny phase	**-3.154**	**0.704**	**-4.479**	**$p < 0.001$**
		Score 6	-1.570	0.890	-1.763	$p = 0.08$
	Swelling type	Conceptive	**-2.368**	**0.620**	**-3.818**	**$p < 0.001$**
		Post-conceptive	N/A	N/A	N/A	N/A
	Female age	Adult	-12.454	5.673	-2.195	n.s.
Solicit mating	Sexual swelling score	Score 5, no shiny	2.024	1.116	1.814	$p = 0.07$
		Shiny phase	**2.268**	**1.119**	**2.026**	**$p < 0.05$**
		Score 6	1.386	1.445	0.959	n.s.
	Swelling type	Conceptive	-17.879	5117.678	-0.004	n.s.
		Post-conceptive	-15.596	10236.776	-0.002	n.s.
	Female age	Adult	16.554	2164.215	0.008	n.s.
Inspect	Sexual swelling score	Score 5, no shiny	0.589	0.444	1.328	n.s.
		Shiny phase	**1.369**	**0.448**	**3.054**	**$p < 0.01$**
		Score 6	0.278	0.579	0.481	n.s.
	Swelling type	Conceptive	-0.011	0.701	-0.016	n.s.
		Post-conceptive	-0.169	1.329	-0.127	n.s.
	Female age	Adult	-0.839	0.578	-1.451	n.s.

Figure 4.1. Male rank during the period of behavioral data collection as determined by Elo scores calculated using all agonistic interactions (supplant, yield, aggression). An individual with a higher Elo score is considered more dominant.

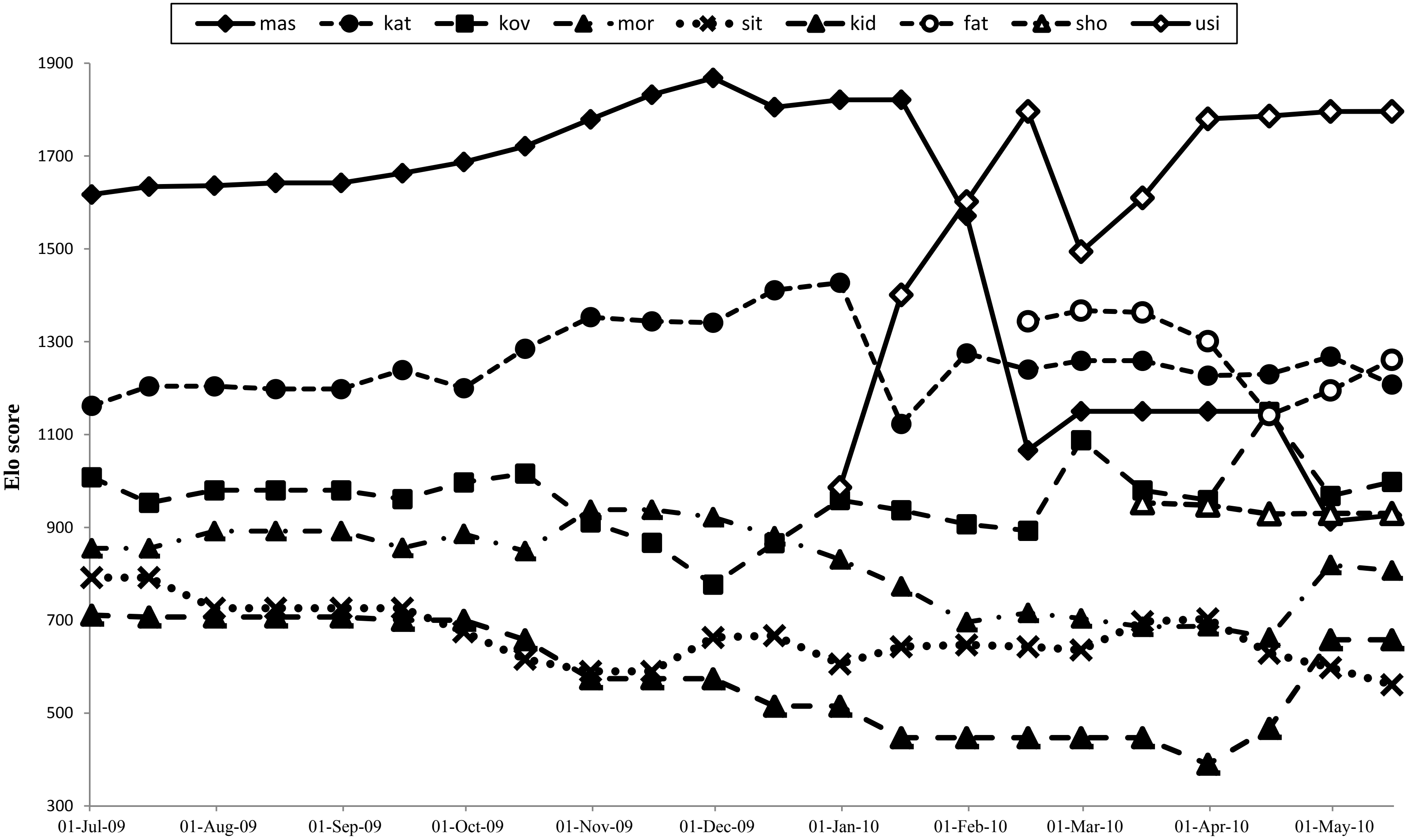


Figure 4.2. Proportion of ejaculatory copulations observed and expected, calculated using the priority of access model per male rank, with females (A) during the period of maximum tumescence, and (B) with females displaying the shiny phase, during the three sub-periods based identity of the alpha males and the stability of the hierarchy. The fit of the data is relatively good for sub-periods 1 and 3, when the hierarchy was stable, but not during sub-period 2, a period of rank instability.

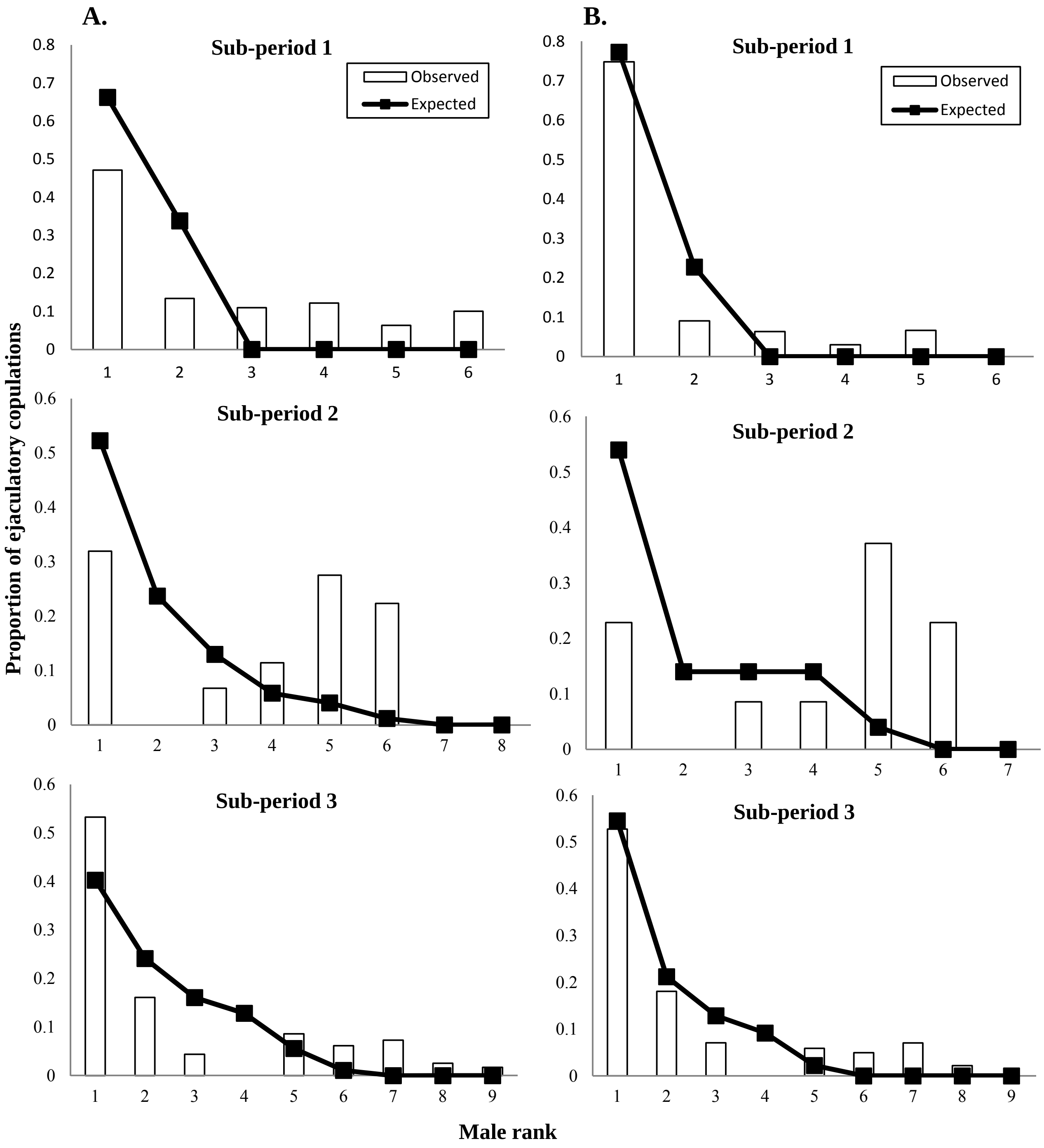
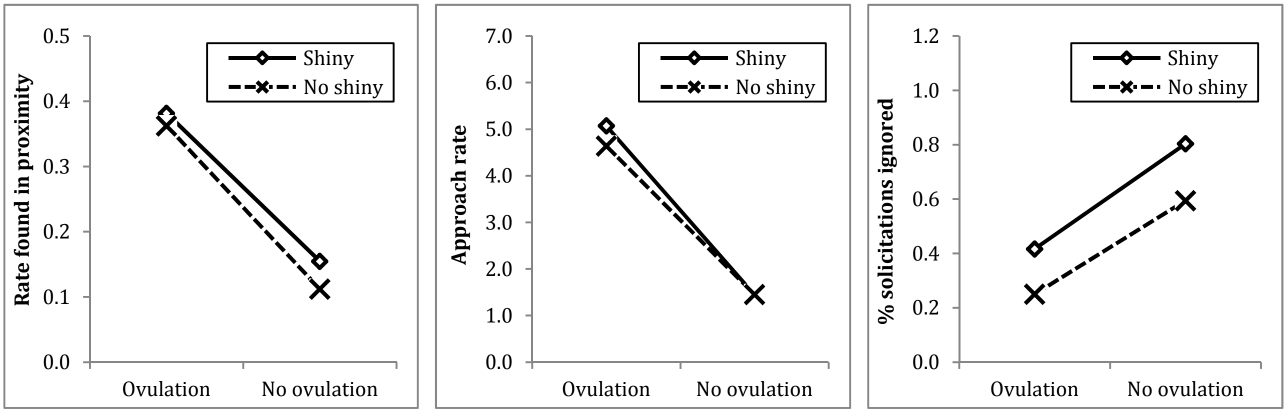


Figure 4.3. Effect of two predictor variables (the ovulatory window and sexual swelling appearance [i.e., the shiny phase]) on behavior of the alpha male (rate found in proximity, approach rate and percent solicitations ignored), as well as the interaction between them.



CHAPTER FIVE:

SUMMARY AND CONCLUSIONS

The main objective of this dissertation was to examine the reproductive characteristics, sexual swellings and mating behavior of wild Sanje mangabeys (*Cercocebus sanjei*). This is only the third study to examine the ovarian endocrinology of a *Cercocebus* species and the first one to do so in a wild mangabey. Here, I present a synthesis of the results, discussion of the significance of this dissertation and outline future avenues of research.

Synthesis of findings

Adult female Sanje mangabeys showed fecal estradiol (fE) fluctuations during the menstrual cycle and reproductive characteristics (i.e., menstrual cycle length, number of cycles to conception, gestation length and duration of post-partum amenorrhea) that were similar to other cercopithecines, including other mangabey species (Gordon et al., 1991; Whitten and Russell, 1996; Walker et al., 2004). Adolescent females had significantly longer menstrual cycles compared to adults. They were also less fertile, as they displayed a period of adolescent sterility (Hartman, 1931), cycling for up to 16 months without conceiving, despite showing fE levels similar to those of adults. No comparable data are available on adolescent fertility in other *Cercocebus* species. Both adults and adolescents exhibited extended periods of sexual receptivity, mating during non-fertile periods of their menstrual cycle and, for adults, also during gestation.

The sexual swellings of the Sanje mangabey provided accurate information on the fE surge, which is used in this study as a proxy for ovulation. In particular, the fE surge occurred when the swelling was at maximum tumescence (MAX), usually within four days of detumescence. Moreover, in most cases examined, the appearance of the swelling skin changed the day prior to the onset of the fE surge, becoming a brighter color (hereafter ‘the shiny phase’), providing an even more precise signal of female fertility. These results are consistent with the graded signal hypothesis which states that sexual swellings indicate when ovulation is more likely (i.e., during the shiny phase) but not its exact timing (Nunn, 1999). This would allow females to concentrate mating behavior with the best male (i.e., the male with the greatest competitive ability) and to confuse paternity among subordinate males that may be of lesser quality.

Different types of sexual swellings, as well as the sexual swellings of adults and adolescent females, varied in their duration of MAX and/or the shiny phase. In particular, conceptive swellings had shorter shiny phases than non-conceptive swellings, and the first swelling post-partum tended to have a shorter MAX period compared to swellings during later cycles. In addition, post-conceptive swellings (i.e., during gestation) were less likely to undergo a shiny phase. Adolescent females, on the other hand, displayed significantly longer shiny phases. These differences may provide cues to males regarding female fertility.

Male Sanje mangabeys displayed a clear dominance hierarchy, with male rank determining access to fertile females. When more than one receptive female was available at a time, alpha males were unable to have complete monopolization. Consequently, as female reproductive synchrony increased and subordinate males gained access to females, male mating skew decreased. Thus, the pattern of male mating skew conformed to the priority of access model (Altmann, 1962); i.e., that rank dictates access to key resources. During a period of rank instability, however, when the two top males in the male hierarchy were deposed by newly arrived males, the pattern broke down, and subordinate males were observed to have increased access to female mating partners compared to dominant males, regardless of the degree of reproductive synchrony.

Dominant males mate-guarded females during the fE surge, as well as during the start of the shiny phase - which coincided with the fE surge - indicating that they were able to assess when the female was most fertile. Accordingly, they also exhibited more interest in females during the shiny phase compared to females during MAX outside the shiny phase. Male Sanje mangabeys also appeared to be able to differentiate among females that were undergoing cycles of differing fertility. In particular, they preferred females during conceptive versus non-conceptive cycles, and the latter over females undergoing post-conceptive swellings. This finding, however, may have been a consequence of the fact that the post-conceptive swellings included in this analysis did not reach MAX or display the shiny phase, although post-conceptive swellings of this species do posses these traits (Chapter 3). Males also preferred adults over adolescent females, presumably because adult females are more likely to conceive and less likely to undergo a period of sterility.

Inter-sexual conflict in the Sanje mangabey

The results of this dissertation demonstrate the occurrence of inter-sexual conflict in the Sanje mangabey. Males attempted to monopolize fertile females by guarding them, while females attempted to mate promiscuously, which has also been observed in other species with similar social organizations (Gowaty, 2004; van Schaik et al., 2004; Stumpf et al., 2011). Male Sanje mangabeys guarded receptive females by blocking the access of the subordinate males, which often prevented the guarded female from mating promiscuously. As most studies have found a positive correlation between male mating success and reproductive success (e.g., Dixson et al., 1993; de Ruiter et al., 1994; Altmann et al., 1996; Vigilant et al., 2001; Widdig et al, 2004; Brauch et al., 2008), it is very likely that mate-guarding is an adaptive male strategy that benefits male Sanje mangabeys by increasing their reproductive success.

Results also showed that males exhibited greater interest in females during the fE surge, as well as during the shiny phase, increasing the frequency of guarding and mating behavior. This suggests that mate-guarding may also give dominant males the opportunity to acquire additional signals about female fertility that subordinate males may not have access to, such as small-scale changes in swelling size or olfactory cues. For example, a study in West African chimpanzees (*Pan troglodytes verus*) demonstrated that males responded to changes in swelling size, with male interest peaking when the swelling was the largest (Deschner et al., 2004). When more than one female was maximally swollen, however, males preferred the female closest to ovulation, suggesting that small-scale changes in size may provide males with additional information on female fertility (Deschner et al., 2004). Similar results have been found in olive baboons (*Papio hamadryas anubis*) (Daspre et al., 2009; Higham et al., 2009). A study of stump-tailed macaques (*Macaca arctoides*) demonstrated that anesthetized males exposed to vaginal secretions collected during the follicular phase of the menstrual cycle showed a significant and sustained increase in circulating testosterone levels, but not when exposed to secretions from the luteal phase (Cerda-Molina et al., 2006). This suggests that males may be able to extract information on female reproductive status from the female's vaginal odor. In the Sanje mangabeys, access to similar signals may have allowed dominant males to pinpoint the ovulatory window and/or distinguish among females undergoing conceptive and non-conceptive cycles. Female Sanje mangabeys display increasing urinary c-peptide levels, a measure of energy balance (i.e., energy intake minus expenditure, Emery Thompson and Wrangham, 2008), and increasing levels of fE during MAX, with each successive cycle approaching conception; the highest levels occur during conceptive cycles (McCabe, 2012). It is possible, therefore, that olfactory cues produced as a result of increasing energy balance or fE level are providing guarding males with information on the fertility of the cycle.

Despite the male reproductive strategy of mate-guarding, it appears that the counterstrategies used by female Sanje mangabeys still enable them to implement their own mating strategies. Females' counterstrategies included prolonged periods of sexual receptivity and the development of the exaggerated sexual swelling. As previously mentioned, dominant males guarded females during the fertile period, particularly during the shiny phase. When more than one female was receptive at a time, however, alpha males were unable to monopolize all of them, so that subordinate males gained access to some females at this time. Moreover, dominant males were not completely successful at guarding females throughout the entire receptive period, and (some) subordinate males were able to mate with females despite the guarding attempts of the alpha male. This, combined with their long periods of sexual receptivity, allowed females to mate with virtually every resident male at some point during each sexual swelling. This strategy benefits females by allowing them to mate promiscuously and confuse paternity among the subordinate males (Hrdy, 1979), who may then provide paternal support that can increase the probability of infant survival, through protection from predation or infanticide (e.g., Taub, 1980; Hrdy, 1981; van Noordwijk, 1985; Harvey and May, 1989; Palombit et al., 1997; Borries et al., 1999), or the provision of other services, such as grooming, playing and tolerance at feeding sites (e.g., Altmann, 1980; Palombit et al., 1997; van Schaik and Paul, 1998; Moscovice:2009dg; reviewed in Alberts and Fitzpatrick, 2012).

Evidence of this benefit comes from studies of baboons (*P. cynocephalus ursinus*) and Hanuman langurs (*Presbytis entellus*), where the risk of infanticide is high, and males that had mated with the female around the time of conception, including putative fathers, did provide protection to the infants (Palombit et al., 1997; Borries et al., 1999; Moscovice et al., 2009). Male Sanje mangabeys, particularly subordinates, have also been observed providing services to females with whom they have mated, including infant carrying and proximity tolerance. It is plausible, therefore, that Sanje mangabey males can exhibit some level of increased parental investment and that female promiscuity is an adaptive counterstrategy to male mate-guarding that enables females to acquire this benefit. It could also be argued that, in addition to extended receptive periods, the development of the post-conceptive swelling may further aid females in confusing paternity, as it was subordinate males that mated most frequently with pregnant females during this study.

In addition to confusing paternity to gain additional services from non-paternal males, females should aim to concentrate paternity in the best male in order to acquire genetic benefits for their future offspring (Cashdan, 1996). Female Sanje mangabeys may be able to achieve this because their sexual swellings are accurate indicators of ovulation, as they develop the shiny phase immediately after the fE surge. In this species, the shiny phase provides males with an even more accurate signal of fertility than the size of the sexual swelling. The shiny phase, therefore, seems to operate in a similar way to the small-scale changes in swelling size described for other species; i.e., signaling the ovulatory window to those males that are in close contact with the female. For example, studies that used photographic techniques to measure small-scale changes in sexual swelling size found that, in olive baboons (*P. h. anubis*) and chimpanzees (*P. t. verus*), the swelling continued to increase in size during the time of ovulation (Deschner et al., 2003; Higham et al., 2008). By advertising this signal, females may be able to ensure that the most competitive male mates during her fertile period and sires her offspring.

Paternity concentration may benefit females in two ways. First, offspring will be more likely to inherit the genes of the male with the highest competitive ability, as dominant males demonstrate greater interest in females during the fertile period. Second, the offspring may receive support from males with high competitive ability, which may increase infant survival. For example, in savannah baboons (*P. cynocephalus*), biological fathers were more likely to support their own offspring in agonistic encounters (Buchan et al., 2003), and the offspring that had biological fathers present in the group for longer reached sexual maturity earlier (Charpentier et al., 2008). Thus, females that sire offspring with the dominant male are more likely to have increased reproductive success. Dominant male Sanje mangabeys have been observed to protect infants harassed by other males, suggesting that biological fathers may have a positive effect on infant survival in this species. It should be noted, however, that paternity data are currently lacking for this study group; therefore, it is unknown whether the dominant male is the father of these infants or if mating success translates into reproductive success.

In summary, this dissertation found further support for the presence of inter-sexual conflict in a cercopithecine primate and in a *Cercocebus* species, in particular. It has been demonstrated that males do not simply mate indiscriminately, as proposed by Darwin (Darwin, 1871), but are, at times, also choosy mating partners, particularly during times of female synchrony. During such times, males concentrate their mating effort on the most fertile female. In addition, this study has shown that despite the male reproductive strategy of mate-guarding, female Sanje mangabeys are able to implement their own reproductive agenda through the use of counterstrategies, such as the development of sexual swellings and long periods of receptivity that allow females to solve the ‘female dilemma’. In particular, these counterstrategies enable females to concentrate paternity in the male with the highest competitive ability, as their swellings provide accurate information with respect to female fertility, while confusing paternity among subordinate males over the course of the long receptive period. These results are consistent with the graded-signal hypothesis.

Future directions

Male mate choice can have significant consequences on male reproductive success. This dissertation has demonstrated that male Sanje mangabeys displayed greater interest in females during their most fertile phase of the menstrual cycle, preferring females during the fE surge, females displaying the shiny phase, as well as those undergoing conceptive cycles. There are other factors that influence female fertility, however, that were not examined in this study, yet that males may use to choose among potential mating partners during periods of female reproductive synchrony. While I did not examine mate choice in relation to female rank, there is evidence that dominance rank has a positive effect on female reproductive success. In Eastern chimpanzees (*P. t. schweinfurthii*), high-ranked females have higher reproductive success compared to low-ranked females as a product of the improved quality of the former’s core home ranges (Pusey et al., 1997). Accordingly, a study of mandrills (*Mandrillus sphinx*) found that males prefer to mate with females of high rank (Setchell and Wickings, 2006). Age may also play a role in male mate-choice, as a study in reindeer demonstrated that long-lived females were more successful at rearing offspring than short-lived females, suggesting that they become better mothers as they age (Weladji et al., 2006). This has also been demonstrated in primates where male chimpanzees preferred mating with more mature females (Muller et al., 2006), who also tended to be of higher rank (Pusey et al., 1997). Female Sanje mangabeys form a dominance hierarchy (McCabe, 2012; Fernández, unpublished); therefore, more detailed analysis of the impact of rank and specific adult age, rather than simply age-class, on male interest would help to determine if these are additional factors influencing male mate-preference.

Rank differences may also explain the relatively high level of variation in several of the reproductive characteristics examined in this study, including cycles to conception after a surviving (3-6 cycles) and a non-surviving infant (1-5 cycles), gestation length (168-179 days), and duration of post-partum amenorrhea (3.8 – 13.3 months). These characteristics may ultimately affect a female's lifetime reproductive success, as they can directly affect the inter-birth interval (Ellison, 2003; Altmann and Alberts, 2005), and each of these parameters can be affected by resource availability. For example, several primate studies have shown that individuals or populations exposed to a better quality diet display faster reproductive rates (Takahata, 1980; Sugiyama and Ohsawa, 1982; Deputte, 1992; Mori et al., 1997; Takahata et al., 1998; Gauthier, 1999; Borries et al., 2001; Altmann and Alberts, 2005). A future study that follows the alpha male, while controlling for the identity and rank of females that are in synchrony, will help us to understand if these other factors are influencing male mate choice in the Sanje mangabey.

A comparison of male preference for females in relation to male dominance rank would help to elucidate whether all males have access to the same information regarding female fertility. Given that the shiny phase is such a conspicuous trait, it is expected that subordinate males will also prefer to mate with females during this time. It is currently unknown, however, whether they have accurate information on the timing of ovulation, or on the probability that a cycle would be conceptive, as dominant males appear to have. It is possible that such detailed information may only be transmitted through repeated and consistent access to females, if, for example, males are using chemical (e.g., olfactory) cues or subtle changes in sexual swelling size within a female's cycle.

During the study, females experienced a period of reproductive suppression from late March through July 2010, which was unexpected. At this time, females exhibited significantly higher levels of fE, accompanied by an interruption in their regular swelling patterns and subsequent sexual behavior. Several studies have related seasonal alterations in the endocrinology and/or behavior of primates to the consumption of certain foods. For example, in female red colobus (*Procolobus rufomitratus*) at Kibale National Park, Uganda, the consumption of foods high in phytoestrogens (i.e., estrogenic compounds synthesized by plants) significantly increased the rates of copulation and aggression among females (Wasserman et al., 2012). Periods of reproductive suppression similar to what was observed in my study have also been described in olive baboons (*P. h. anubis*: Higham et al., 2007), chimpanzees (*P. t. schweinfurthii*: Emery Thompson et al., 2008) and Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*: Lu et al., 2011). In all three studies, reproductive suppression was associated with an increase in progesterone and a drop in estrogen during a period characterized by the consumption of the fruit of *Vitex spp.* Sanje mangabeys have been observed consuming ripe *Vitex doniana* (McCabe, 2012); however, whether this fruit is a significant part of their diet during the period of reproductive suppression remains to be investigated. Furthermore, it should be noted that female Sanje mangabeys exhibited elevated, rather than decreased, fE levels during this period of amenorrhea, contrary to the aforementioned studies; thus, it is possible that this phenomenon is caused by other factors (Wasserman et al., 2012). Regardless, further study is required to determine if this period of reproductive suppression is an annual event, and if so, the affect it may have on interbirth intervals and other life-history traits of this species.

A major assumption of this research has been that female Sanje mangabeys prefer to have the dominant male sire their infants, as has been observed in most other primate species (reviewed in Manson, 2007). However, this is not necessarily the case. There is evidence to indicate that female primates may use other criteria to select mates, such as males with higher gene compatibility (Mays and Hill, 2004; Schwensow et al., 2008; Setchell et al., 2010), recent immigrant males (Boinski, 1987), or males with brighter coloration (Setchell, 2005). To date, no studies on female preference in *Cercocebus* have been undertaken, but research on chimpanzees (*P. t. verus*) and orangutans (*Pongo pygmaeus*), where there is a high degree of sexual dimorphism and male coercion is common, have shown that females seem to be able to exercise their mate preference through a mixed mating strategy (Stumpf and Boesch, 2005) by being more selective during the time of ovulation, and less so outside this period (Stumpf and Boesch, 2005; 2006; Knott et al., 2010; but see Muller et al., 2011). Female Sanje mangabeys do solicit mating with non-guarding males throughout their receptive period when the guarding male is not in view, suggesting that they may prefer males other than the dominant as fathers. An examination of variation in female solicitation frequency during the time of ovulation as well as across males will be crucial to understanding the mating preference of female Sanje mangabeys.

Alternatively, females may be relying on cryptic female choice (Thornhill, 1983); i.e., the differential utilization of sperm from different males (Birkhead and Kappeler, 2004). Cryptic female choice is well documented in insects, but it has also been shown in bird species where extra-pair copulations are common and males may coerce females into mating with them. In the feral fowl (*Gallus gallus*), for example, females mate with multiple males, but they are less likely to eject the sperm of dominant males compared to that of subordinates (Pizzari and Birkhead, 2000). Cryptic female choice is poorly documented in primates, but the similarities that exist in behavior (e.g., male guarding, female promiscuity) and morphology (e.g., sperm plugs, sperm morphology) between birds and primates suggests that it may be an important adaptation that allows females to implement a counterstrategy to male mating behavior in some species (Reeder, 2003; Birkhead and Kappeler, 2004). Obviously, demonstrating cryptic female choice would require invasive procedures that cannot be performed in field settings. Nonetheless, a careful comparison of females' distribution of mating solicitations and rejections during the peri-ovulatory period, as well as outside this period, combined with a study of male mating success and how that relates to the probability of the male siring a female's offspring, would help us to better understand female mate choice and the ability of females to utilize this strategy.

Although males are typically considered the sex that will compete over access to mates given their lower reproductive investment and higher reproductive variance compared to females (Trivers, 1972), under certain circumstances, such as when males, the services they can provide and/or their sperm are limited, females are also predicted to compete over mates (Drea, 2005; Clutton-Brock, 2009; Rosvall, 2011; Stockley and Bro-Jørgensen, 2011). For example, paternal care can positively affect an infant's survival and subsequently, a male's reproductive success (Buchan et al., 2003; Charpentier et al., 2008), but it may need to be divided among all the females with which a male has mated (Altmann et al., 1977; Breiehagen and Slagsvold, 1988; Bensch and Hasselquist, 1994; Slagsvold and Lifjeld, 1994; Gowaty, 2004). As such, there is evidence from a wide variety of taxa, including primates, that females compete over the 'best' males (Drea, 2005; Clutton-Brock, 2009; Rosvall, 2011; Stockley and Bro-Jørgensen, 2011). For example, female primates have been shown to compete through the use of rank, where high-ranking females displace the lower-ranked females from male ‘friends’ (Palombit et al., 2001) through direct aggression, in order to interrupt copulations and/or solicitations (Sommer, 1989; Bercovitch, 1995; Vervaecke et al., 2003); suppress reproduction by increasing stress (Bowman et al., 1978; Dunbar, 1980; Wasser and Starling, 1988; but see Kuester and Paul, 1996), or to provoke miscarriage (Wasser and Barash, 1983; Wasser and Starling, 1988). Females may even mishandle or attack newborns of ‘rival’ females (Silk, 1980; Digby, 2000; Kleindorfer and Wasser, 2004; Townsend et al., 2007). Finally, some females may synchronize their receptive period (Doran-Sheehy et al., 2009), or conspicuously advertise their quality to become more attractive to males (Haselton et al., 2007; Dubuc et al., 2009; Alberts and Fitzpatrick, 2012), in order to deplete the sperm available to other, less attractive females (Small, 1988; Doran-Sheehy et al., 2009). In baboons, years with a more female-biased sex ratio had a significant increase in female-female aggression (*P. h. ursinus*: Cheney et al., 2012), and guarded females received more female aggression than non-guarded females (*P. ursinus*: Huchard and Cowlishaw, 2011). Female Sanje mangabeys did exhibit aggressive behaviors towards one another, although it is not currently known if the frequency varied in relation to the socio-ecological conditions or the level of reproductive synchrony. Examining the pattern of female-female aggression in relation to female reproductive status, the identity of the guarding male, and at various degrees of synchrony will help shed light on the role of female mating competition in female social relationships among primates (Cheney et al., 2012).

Significance of this dissertation

This dissertation contributes to the accumulation of our knowledge on the understudied genus *Cercocebus*. As such, it provides the first ever description of the sexual and mating behavior, ovarian endocrinology and reproductive characteristics of the Sanje mangabey, and of a wild *Cercocebus* species. This study, has also provided further evidence that inter-sexual conflict occurs in primates, that male and female reproductive strategies are far more nuanced than the traditional sex roles described by Darwin (Darwin, 1871), and that males and females have evolved complex behavioral, physiological and endocrinological adaptations to gain an advantage over the opposite sex and improve their own reproductive success (Stumpf et al., 2011).

The results of this study can be used to aid in the conservation of this Endangered primate (Ehardt et al. 2008). Now that an habituated group with identified individuals is available, continued long-term monitoring should be established to obtain additional life-history data, such as inter-birth interval and age at first reproduction. This would also provide a continuous presence at the site, which has been shown to deter illegal activities, such as poaching, that does occur in the area, including within the group's home range (Fernández and McCabe, unpublished). With an estimated population size of between 1,300 and 3,500 individuals divided into two isolated populations (Ehardt et al., 2005; Rovero et al., 2009), information regarding their reproduction, and in particular, life history parameters, are necessary to estimate the viability of the Sanje mangabey population and to design and implement specific conservation management plans for this species (Dobson and Lyles, 1989; Strier et al., 2006).

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APPENDIX

ETHOGRAM OF RECORDED BEHAVIORS

Sexual behaviors

Copulation	Mount accompanied by intromission and pelvic thrusting
Ejaculation	A mating male freezes momentarily after several thrusts, marking the end of the copulation
Female moves	A female mating rejection consisting of the female walking away from a male after a hip-grasp
Hip-present	A female mating solicitation, during which a female lifts her tail and walks past or walks in front of a male, stopping one or two meters in front of the male's face and displays her rump to the male. The female may or may not look back at the male
Hip-grasp	A male mating solicitation, in which the male grabs both hips of a female – may or may not be followed by a mount
Ignores	A male mating rejection, in which the male does not mount the female after a hip-present. The male may or may not inspect the female
Inspect	A male visually inspects and/or sniffs the sexual swelling of a female
Mount	Holding an individual's hips with both hands, an individual stands on its hind limbs and proceeds to thrust
Thrust	Rhythmic movement of the pelvis by the mounting individual

Social behaviors

Aggression	Any event that involves an individual pushing, biting, pulling the tail of, or jumping on top of another individual, or any other physical aggression that is not a chase
Approach	An adult individual moves from beyond 5 meters from another individual into a proximity of less than 5 meters
Leave	An adult individual moves from within 5 meters of another individual to a distance beyond 5 meters
Groom	Inspecting and combing the pelage and/or skin of another individual using fingers, hands and occasionally the mouth or teeth

Chase	An individual runs behind another individual in an aggressive manner, usually accompanied by screaming
Present	An individual turns and walks backwards towards another individual, often accompanied by looking back at the target
Supplant	A sitting individual moves away as another individual approaches and takes the former’s spot
Yield	A walking individual stops and remains still until another individual that is moving towards the same location, or that stands in the way of the former individual, walks away