

## INTERFERING WITH OTHERS: FEMALE-FEMALE REPRODUCTIVE COMPETITION IN *PAN PANISCUS*

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### INTRODUCTION

Compared to males, females traditionally have been considered less sexually strategic because their relative gain from competitive reproductive tactics and strategies has been thought to be evolutionarily insignificant [see Hrdy, 1981, 1999a]. Recently, it has become increasingly clear that the variation in female reproductive success, if lower than in their male counterparts [e.g., Kuester et al., 1995], may be sufficient to have evolutionary consequences [Hrdy, 1984, 1999b]. Females can influence their reproductive success through a variety of behavioral tactics and strategies such as competition over access to mates and access to other resources contributing to inclusive fitness (e.g., food or helpers) [Dunbar, 1988]. In addition, females can interfere with the reproduction of others [Hrdy 1984, p 109], thereby gaining immediate or future benefits, the so-called **return benefit spite** hypothesis [Trivers, 1985]. Further, males have been observed to show mate selectivity [Kuester & Paul, 1996], suggesting that female quality varies. Thus, the traditional focus on male intrasexual competition and female intersexual choice can be complemented by female-female competition and male mate choice [Robinson, 1982; Kuester & Paul, 1996; Cunningham & Birkhead, 1998].

Intrasexual reproductive competition can be expressed by choices made in one's own lifetime as well as by the influence on or restriction of choices in the lives of others [Hrdy, 1999b; Trivers, 1985, p 25]. Ultimately, both modes of competition may have reproductive benefits. The benefits of each option may vary according to an individual's position or role in a certain social condition [Hrdy 1999b]. Just as for males, the reproductive choices made by females should vary according to individual characteristics such as age and physical condition (e.g., nutritional or reproductive state), and several studies have shown that female dominance rank may influence lifetime reproductive success [Dunbar, 1980; Harcourt, 1987; Pusey et al., 1997; Pusey, 2001].

We can expect that dominant individuals or the dominant sex will be less constrained in the expression of reproductive competitive tactics and strategies. By this reasoning, female bonobos (*Pan paniscus*) provide an interesting case for studying

interference strategies. First, female bonobos can dominate males [Vervaecke et al., 1999a] so that the expression of female intrasexual competition is expected to be less constrained by the opposite sex. Second, dominance hierarchies are clearly measurable among female bonobos [Vervaecke et al., 1999a; Franz, 1998]. While dominance relations in chimpanzee females (*Pan troglodytes*) are much less pronounced, inter-female competition has nonetheless been shown to have important reproductive consequences in this sister species as well, and dominant female chimpanzees may use infanticide as a strategy to influence other females' reproductive success [Pusey et al., 1997; Pusey, 2001].

The life history tactics of large bodied primates are characterized by a relatively low reproductive potential due to long reproductive cycles, few offspring, late maturation, and a prolonged period of social learning [Bronson, 1989; Charnov & Berrigan, 1993]. Crucial is the fact that subtle reproductive gains may be proportionately more important for females than for males given the basic inequality in lifetime reproductive potential between the sexes [Trivers, 1972; Bateman, 1948]. In this chapter we provide preliminary data suggesting that bonobo females interfere with other females' reproductive success. We advance the view that female-female competition is a significant feature of this species, consistent with ideas developed by van Schaik [1989] and Sterck et al [1997] emphasizing the role of competition in the social evolution of primate females. We review the theoretical literature on female-female competition where it clarifies interpretations of our observations, suggesting that the observations presented in this chapter, previously undescribed for bonobos, are worthy of intense investigation.

## **THEORETICAL VIEWPOINTS ON FEMALE-FEMALE COMPETITION**

### **Interfering With Reproductive Cycles: Cycle Synchrony and Reproductive Inhibition**

Females may influence other females' reproductive success by interfering with their competitors' reproductive cycles. Females are sensitive to signals from the ecological as well as the social environment that may determine the optimal timing of reproduction [Imms, 1990], and ecological signals may be responsible for reproductive seasonality in primates [Wallis, 2002; Nunn, 1999a]. In addition, social signals can synchronize female ovarian cycles, a phenomenon that has been documented in several species [rodents: McClintock, 1984; *Pan troglodytes*: Wallis, 1985; *Homo*: McClintock, 1971].

Reproductive inhibition of lower ranking animals is another potential mode of reproductive competition among females [Dixon, 1998; Abbott, 1991]. McClintock [1981, 1983] has suggested that the cycle of a dominant individual might act as a "zeitgeber" (an environmental cue) for menstrual cycle synchrony, with the dominant female signaling to subordinate females to fine-tune their reproductive physiology. Pheromones have been suggested as proximate regulatory factors for female cycle synchrony in humans [e.g., Stern & McClintock, 1998]; however, it is unclear whether dominant females impose pheromonal control or whether subordinate individuals use pheromonal cues to avoid investment in offspring in a socially adverse climate [Hrdy,

1999b]. Apart from mechanisms involving aggression-induced stress [De Vleeschouwer, 2000; De Vleeschouwer et al., 2001], the mechanism and exact nature of these phenomena still awaits demonstration in non-human primates. Pheromonal influences, however, are believed to operate among cooperatively breeding callitrichids (marmosets and tamarins), where breeding female group members compete over extra helpers for infant care [see Dixson, 1998; Epple and Katz, 1984; Savage et al., 1988]. Reproductive inhibition also has been demonstrated in taxa other than callitrichids. In talapoin (*Miopithecus talapoin*), low ranking females often are the victims of aggression [Bowman et al., 1978]. In yellow baboons (*Papio cynocephalus*), female coalitions are often directed at low-ranking females in the follicular phase of the menstrual cycle, resulting in an increased number of cycles to conception and a longer interbirth interval [Wasser & Starling, 1988; for other examples of reproductive inhibition see Dixson, 1998].

### Interfering With Copulations

Females can limit the reproduction of other females by interfering with copulations. Sperm of high quality may be limiting; thus, competition may arise among females for this resource [Hrdy, 1974, 1977; Small, 1988; Sommer, 1989; Bruce & Estep, 1992]. Female sexual interference has been reported in more than 30 primate species [reviewed in: Niemeyer & Anderson, 1983; Smuts, 1987; Dixson, 1998]. Theoretically, two forms of mating interference have been distinguished: harassment and interruption of copulation. Harassment occurs when relatively mild interferences occur, such as approaching and touching or slapping the recipient, acts which do not necessarily lead to termination of copulation [Bruce & Estep, 1992; Dixson, 1998]. Ultimately, these actions will have no selective effect unless they induce stress which may interfere with female reproductive physiology (e.g., ovulation or implantation, see Saltzman, this volume) or male sexual response (e.g., capacity to ejaculate). Harassment may also increase the duration of the copulatory sequence, thereby exposing the pair *in copula* to predation. Interruption of copulation is more disruptive and leads to termination of the copulatory sequence [Bruce & Estep, 1992; Dixson, 1998]. The **reproductive potential hypothesis** [Niemeyer & Chamove, 1983] or **sexual competition hypothesis** [Drukker et al., 1991] considers interference with copulation to be a tactic to reduce the reproductive potential of competitors. There need not be immediate advantages to females from interfering with others' copulations; however, these acts may yield future benefits [the **return benefit spite hypothesis**: Trivers, 1985].

The **resource competition hypothesis I** [Niemeyer & Anderson, 1983] states that interference with copulations functions to diminish competition over limiting resources. This hypothesis predicts that a female may influence the number of offspring in a birth cohort competing over resources with her own offspring. Where another female's conception could not be interrupted, a female may still influence the sex ratio of a birth cohort by way of differential harassment of mothers pregnant with sons or daughters [Silk, 1983; Silk et al., 1981]. Such behavior, by which females can benefit in terms of future survival or reproduction by present spiteful behavior to other females, can also be classified as a form of **return benefit spite** [Trivers, 1985; Brereton, 1994].

**Interfering With Reproductive Output: Infant Handling, Harassment, and Infanticide**

A third competitive strategy females can use is to interfere in the raising of other females' offspring, such as by indirect (i.e., enforced neglect or harassment of the mother resulting in an infant's death) or direct infanticide (i.e., cases where infants die as the result of physical aggression [Digby, 2000]). Direct infanticide by females has been observed in at least five species of primates [reviewed by Digby, 2000]. Pusey et al. [1997, p 830] describe infanticide in free-ranging chimpanzees as "a significant, if sporadic threat, rather than the pathological behavior of one female." According to the **sexual selection hypothesis**, infanticide can theoretically benefit the sex whose reproductive success is limited by access to the opposite sex by freeing the caregiver of the infant to mate with the individual that killed the infant [Hrdy, 1974, 1979]. In this strict definition, the hypothesis is only expected to apply to females in those species where males are the limiting factors for infant survival and where females compete for access to mates, similar to some birds [reviewed by Digby, 2000]. Two other hypotheses for direct infanticide have been formulated. By killing other females' offspring, the infanticidal female and her young will have fewer present and future competitors for limiting resources such as food or access to helpers [**resource competition hypothesis II**: Hrdy, 1979]. The **exploitation hypothesis** [Hrdy, 1979] suggests that infanticidal females benefit from use of the victim either in terms of nutritional value by consuming the infant, in terms of a buffer against aggression from others, or as a tool to gain maternal experience [Digby, 2000].

Indirect infanticide has been documented in at least 15 species of primates, including prosimians, New World monkeys, and Old World monkeys [Digby, 2000; Silk et al., 1981; Dixson, 1998]. In many primates, females show interest in infants of other females, and the distinction between infant care and infant abuse is not always clear-cut [Nicolson, 1987]. Infant handling can result in indirect infanticide in case of prolonged separation from the mother resulting in starvation or dehydration [Hrdy, 1976]. In this case infant handling may be a form of **reproductive competition** [Hrdy, 1976; Wasser, 1983; Silk, 1999]. The **exploitation hypothesis** [Hrdy, 1979] suggests that females benefit from use of the victim in terms of a buffer against aggression from others or as a tool to gain maternal experience [Digby, 2000]. Other hypotheses regarding infant handling have been formulated such as **byproduct of selection for appropriate maternal care** [Silk, 1999] and the **phenotypic manipulation hypothesis** [Jones, 1986].

**METHODS****Animals, Study Sites, and Procedures**

Bonobos are found living in large fission-fusion communities [reviewed in Van Elsacker et al., 1995] in tropical rainforests of the Zaire basin in the Democratic Republic of Congo [Thompson-Handler et al., 1995]. Mating is generally considered promiscuous and opportunistic [Kano, 1992], and mating tactics such as consortships or monopolization by dominant males, reported for chimpanzees [Tutin, 1979], appear absent in bonobos [Kano, 1982; but see Gerloff et al., 1999]. Recently, however, males of high dominance rank have been found to have higher mating [Kano, 1996] and reproductive

success [Gerloff et al., 1999], suggesting that variance in reproductive success among male bonobos may be higher than previously assumed. Males remain in their natal group and rely heavily on maternal support in social conflict situations [Kano, 1992]. Females, on the other hand, migrate to other groups when they reach sexual maturity [Furuichi, 1989; Idani, 1991]. It has been confirmed by genetic analysis of populations that, within communities, males are relatively closely related, while females are not [Furuichi et al., 1998; Gerloff et al., 1999; Hohmann et al., 1999]. Yet, recently, Hohmann [2001] also reported an instance of male immigration in an existing community. Frequent non-reproductive sexual contacts between and within both sexes have been related to social bonding and tension reduction [Parish, 1996; Parish & de Waal, 2000; de Waal, 1987] (Figure 1). Takahata et al. [1996] stress the potential for female-female competition in bonobos given the general lack of kinship among adult female group members. These authors suggest that female genito-genital (GG) rubbing and prolonged swelling periods developed to reduce social tension. To date, studies on female bonobos have focused primarily on bonding mechanisms [e.g. Idani, 1991; Parish 1993, 1996; Parish & de Waal, 2000], yet we believe competition may be a significant feature of interfemale relationships in this species.



Figure 1. Young female bonobos of the Planckendael group playfully engaging in social sex. (Photo by Peter De Ridder).

**Table I. Identity of study animals per group.**

Name	Sex	Date of birth	Place of birth	Sire x Dam
<b>Wuppertal</b>				
Mato	M	12/22/63	Frankfurt	Camillo x Margrit
Lisala	F	04/24/80	Stuttgart	Masikini x Catherine
Lusambo	M	07/21/80	Stuttgart	Masikini x Kombote
Birogu	M	08/11/89	Wuppertal	? x Catherine
Eja	F	07/14/90	Frankfurt	Bono x Daniella
Bondo	M	09/17/91	Wuppertal	? x Lisala
Opala	F	04/08/98	Wuppertal	? x Lisala
<b>Apenheul</b>				
Mobikisi	M	± 1981	Congo	?
Jill	F	07/15/85	Yerkes	Bosondjo x Laura
Molaso	F	± 1985	Congo	?
Mwindu	M	± 1985	Congo	?
Rosie	F	± 1989	Congo	?
Zuani	F	± 1990	Congo	?
Hani	M	± 1990	Congo	?
Lomela	F	05/19/92	Frankfurt	Bono x Daniella
Liboso	F	01/17/98	Congo	Hani x Zuani
Tarishi	M	09/17/98	Apenheul	? x Jill
Kumbuka	F	07/09/99	Apenheul	? x Molaso
<b>Planckendael</b>				
Desmond	M	± 1970	Congo	?
Dzeeta	F	± 1971	Congo	?
Hermien	F	± 1978	Congo	?
Hortense	F	± 1978	Congo	?
Kosana <sup>a</sup>	F	± 1980	Congo	?
Kidogo	M	02/28/83	Stuttgart	Masikini x Catherine
Ludwig <sup>b</sup>	M	08/24/84	Antwerp	Desmond x Dzeeta
Redy	M	10/24/90	Planckendael	Desmond x Hortense
Unga	F	02/02/93	Planckendael	Desmond x Hermien
Vifjo	M	07/23/94	Planckendael	? x Hortense
Zómi	F	01/28/98	Planckendael	? x Hermien
Zamba	M	04/16/98	Planckendael	? x Hortense
<b>Stuttgart</b>				
Kombote	F	1965	Congo	?
Masikini	M	1966	Congo	?
Daniela	F	06/17/68	Frankfurt	Camillo x Margrit
Diatou	F	10/21/77	Stuttgart	Masikini x Catherine
Kuni	F	02/24/85	Stuttgart	Masikini x Kombote
Kichele	F	04/19/89	Stuttgart	Masikini x Diatou
Eya	F	07/14/90	Frankfurt	Bono x Daniela

Table I. (continued)

Name	Sex	Date of birth	Place of birth	Sire x Dam
<b>Twycross</b>				
Diatou	F	10/21/77	Stuttgart	Masikini x Catherine
Kakowet II	M	06/07/80	San Diego Zoo	Kakowet x Linda
Jasongo	M	08/02/90	Wuppertal	Mato x Lisala
Banja	F	02/01/90	Köln	? x Bonnie
Kichele	F	04/19/89	Stuttgart	Masikini x Diatou
Keke	M	01/02/94	Twycross	Kakowet x Diatou
Yasa	F	08/27/97	Twycross	Kakowet x Diatou
Kinshasa	F	10/19/01	Twycross	? x Banja

<sup>a</sup>Moved from Planckendael to Frankfurt in May 1999; <sup>b</sup>Moved from Leipzig to Planckendael in June 1999; ± - Date of birth unknown (estimate) [see Leus & Van Puijenbroeck, 2001]; ? - Unknown parent

We investigated whether captive female bonobos influence the reproductive success of other females 1) by interfering with reproductive cycles, 2) by interfering with their copulations, and 3) by interfering in reproductive output. Data were gathered in several captive bonobo groups (see Tables I & II for study sites and group compositions). Various research questions were addressed, but a standard observation protocol was used to score all occurrences of agonistic and sexual behaviors [described in Vervaecke, 1999; Stevens, 2000]. The *ad libitum* cases we report in this chapter derive from our main studies using an *a posteriori* theoretical framework regarding female reproductive interference competition reviewed above.

To evaluate menstrual synchrony, we used the guidelines of Wilson [1992] and Weller and Weller [1997]. According to this method, the start of the first menses of female A is compared with the first and second start of menses of female B. Subsequently, the start of the first menses of B is compared with the start of the second menses of A. The smallest of the three values is the absolute difference between A and B. This difference is determined for all cycles. The smallest possible absolute difference is 0 (i.e., both females have menses on the same day), and the largest is 17 (using an average cycle length of, for example, 34 days). If, for two of the three cycles, the absolute difference is smaller than the cutoff point, there is synchrony for these two females. The cutoff point is found by dividing the cycle length by four. Since, for each female, based upon three menses, only two cycle lengths can be determined, Weller et al [1999] used the average of the two cycle lengths to determine the first cutoff point. If two females have two similar cycle lengths (e.g., 34, 35, or 36 days), the resulting cutoff points are 8.5, 8.75, or 9 d, respectively. If two females have a different average cycle length, the cutoff point per cycle for each female is added to the cutoff point of the other female and divided by two. Absolute differences in timing of menses smaller than

**Table II. Observation period per study group.**

Group	Year of Study	Number adult males	Number of adult females	Number of juveniles & infants	Number of study hours
Planckendael	1992-1999	3	4	3	1218
Wuppertal	1999	4	2	1	203
Apenheul	2001	3	5	3	494
Stuttgart	1991 & 1994	1	3	3	82 & 120
Twycross	2001	2	3	3	302

the cutoff point represent synchrony, values larger than the cutoff point represent asynchrony.

The swelling cycle of bonobos is somewhat different from that in chimpanzees in the sense that bonobo females exhibit swelling throughout 70% of their cycle [Vervaecke, 1999]. In bonobos, then, ovulation is not as reliably placed within the swelling phase compared to chimpanzees, and swelling synchrony is not an indicator of ovulatory synchrony. Menses, however, are very good *post hoc* indicators of ovulatory synchrony in bonobos due to the consistency in the length of the luteal phase [Vervaecke, 1999].

## RESULTS

### **Interfering with Reproductive Cycles: Cycle Synchrony and Reproductive Inhibition**

An apparent case of menstrual synchrony in bonobos was documented among three adult females of the Planckendael study group [Vervaecke et al., 1999b]. Two females, Hermien and Dzeeta, showed first postpartum menses simultaneously with regular menstruation of the alpha female (Dzeeta), possibly acting as a "zeitgeber." The second ranking female, Hermien, menstruated during the menses of the alpha female. The third ranking female, Hortense, did so three days later. They exhibited the first postpartum menses within days of each other, although Hortense's last infant was born one year after Dzeeta's and Hermien's [for this group's composition see Leus & Van Puijenbroeck, 2001; see Wallis, 1985, 1992, 1994 for a discussion of postpartum swelling onset in *Pan troglodytes*]. Zinner et al. [1984] showed that the probability of conception in hamadryas baboons (*P. hamadryas*) decreased if swelling phases coincided and argued that sperm may be a limiting resource, a condition that would benefit dominant females.

Dzeeta's inter-menstrual interval (IMI) was 30.71 d (73 cycles; range = 21-45 d, standard deviation = 3.63 d). Hermien's IMI was 43.20 d (5 cycles; range = 36-55; standard deviation = 8.47 d), and Hortense's IMI was 37.75 d (16 cycles; range = 24-52 d; standard deviation = 7.90 d). In our 10-year study of this group, it was rare for two or three females to exhibit a cycle of regular swelling lasting three or four months. Females



in our group were generally pregnant or lactating. Since bonobo females exhibit only a few ovulatory periods during their lifetimes, this case is significant because it demonstrates that females with different IMI's displayed synchronous menses during their first postpartum cycle.

Recently, another case of menstrual synchrony was observed in the Planckendael study group. Dzeeta suffered a stroke in the first half of 2001 and failed to show regular swelling cycles or normal tumescence, her labia being asymmetrically wrinkled and bluish-colored. In addition, she lost her alpha position to Hermien. Hermien resumed maximal swelling and menses on 29 March 2001 after the birth of her last infant. Hermien menstruated on 5 September 2002, and Hortense did so on the 11<sup>th</sup> of that same month. In December 2001, Hermien menstruated on the 18<sup>th</sup> and 19<sup>th</sup> of December, and Hortense menstruated on the 19<sup>th</sup> of December. The menses between September and December was, unfortunately, not recorded. Nonetheless, these observations provide further evidence for menstrual cycle synchrony in bonobos. See De Ridder [2001] for four additional cases of apparent postpartum menstrual cycle synchrony in *Pan paniscus*.

Females may also inhibit other females' reproductive cycles. In 1999, an adult bonobo female, Kosana, was introduced in the Planckendael group. For the first two years she failed to show any sign of swelling cycle or menstruation. Especially in the first year after introduction, she was often the victim of aggression by two of the resident females. These two females also formed coalitions against Kosana, who showed many signs of distress, such as frequent grinning and pacing, and who was usually located in the periphery of the group. The group's sub-adult female, 6 years old at the time, also harassed the newcomer frequently. Although the new female was of proven fertility and despite the fact that she regularly mated with all of the group's males, she did not become pregnant. In the second year after introduction, the new female started to show affiliative bonds with one of the females and by the end of that year she seemed fully integrated. Kosana spent much time with the other females and, during feeding sessions, was allowed to forage proximal to them. Only after this bonding had begun did she resume menstruating, showing a regular swelling cycle. After two normal swelling cycles this female became pregnant.

### **Interfering With Copulations**

We studied sexual interference in Planckendael. At the time, the group consisted of three adult females, three unrelated adult males, and one adolescent male. The group was studied for 5.5 months (1218 h, Table II) covering two menstrual cycles for each of the three adult females. Copulations (defined as mount with intromission [penis in vagina]) were relatively rare (26, 13 and 8 for three females over the entire study period) compared to other sexual interactions (presentations: clearly showing the genitals to another individual without subsequent sexual interaction [n=105]; non-copulatory mounts: mount without intromission of the penis in the vagina [n=102]). In 9% of these interactions, other adults interfered aggressively. We observed that females, generally the dominant female (n=12), performed 14 out of 23 (61%) sexual interferences. In four instances the alpha-female clearly aggressed the female of the dyad. She behaved in an unusually aggressive manner when the second ranking female was copulating with the



lowest ranking male (e.g., pulling the female off the male while biting her and chasing her around). In all cases of interference by the alpha female, copulation was immediately terminated and copulation partners separated [Vervaecke & Van Elsacker, 2000].

Similarly, in a three-month study of a group of five adult females and three adult males in Apenheul, seven cases of female sexual interference were observed [494 h observation, Stevens, unpublished data, Table II]. In six of these cases, the alpha female approached the lowest ranking female when she was mating with the highest ranking male or the lowest ranking male or when they were about to mate. These latter inferences were based upon observations of mutual sexual presentations and approaches. Here, too, the result was disruption of the incipient copulation, although the alpha female in this case behaved less violently than the Planckendael female. Another high-ranking female also interfered in copulations of the lowest ranking female, after which the copulation ended. In free ranging bonobos, female harassment of copulations has been observed as well. Females were involved in 6 out of 33 (18%) documented cases of sexual interference [Kano, 1992].

#### **Interfering With Reproductive Output: Infant Handling, Harassment, and Infanticide**

Hitherto, no direct female infanticide has been reported for bonobos. In every bonobo group considered for the present chapter (Table II), infant handling by females was common and ranged from carrying infants to outright aggression directed at them (see Table III). In Wuppertal, the adolescent female, Eja, carried the infant of the alpha female Lisala. The mother nervously followed Eja around and tried to retrieve her infant. Similarly, in Planckendael, the dominant female, Dzeeta, carried infants of the lowest ranking female, Hortense. Dzeeta, who had no infants of her own, held Hortense's first male infant for several hours, ignoring the continuous efforts of the mother to retrieve the infant. The same behavior was repeated with Hortense's next infant in an episode lasting at least an hour. In Frankfurt, Ukela attempted to pull the infant of Salonga away in tugging periods lasting up to thirty minutes (M. De Lathouwers, personal communication). In some cases, mothers were unable to retrieve their infants themselves for long periods of time, and the perpetrators had to be anesthetized to return the infant to its mother. In Apenheul, Molaso, a nulliparous female, kidnapped the 2-month-old Liboso from its mother, Zuani, although the latter was higher ranking. The trio was separated from the group and, the next day, the kidnapping female was anesthetized to take the infant and render it to his mother. Nine days later, Molaso again took the infant but allowed the mother to retrieve it after a few seconds (R. Bakker, personal communication). These observations support Neugebauer's [1980] report of an infant kidnapping by a dominant female who had lost an infant. Similar to our experiences, the kidnapper required anesthetization in order to return the infant to its mother.

In October 2001, the alpha female at Twycross Zoo, Diatou, kidnapped the first-born infant of the lowest ranking female, Banja [Stevens et al., unpublished data]. Diatou was still nursing her own four-year-old daughter and nursed the new infant for six weeks. Although Diatou had always been a very caring mother for her own three offspring, she was remarkably rough with this new infant. She would often push the

infant around or leave it crying beside her on the floor. After six weeks, Diatou seemingly lost interest in the infant. During group excitement, she would drop it on the floor and, on one occasion, Kichele, Diatou's eleven-year-old daughter, carried the baby around for more than an hour before Diatou came to retrieve it. Since the baby showed signs of weakness and dehydration, the baby was removed for human rearing. During the whole period, Banja was mildly interested in the baby but did not attempt to retrieve it. Since no human observer witnessed the actual birth, the circumstances under which Diatou took the baby away from Banja are unknown.

In addition, we witnessed two cases of direct aggression by females towards an infant of another female. In Planckendael, the highest-ranking female, Dzeeta, aggressively clashed into Hermien's ventrum where her newborn infant, Unga, was clinging. In Stuttgart, we observed how the dominant female, Kombote, threw Kichele, Diatou's nursing infant, against a wall. In none of these cases did the infants suffer visible harm, but the potential for injury and severe distress was evident (Table III, cases 6 and 8). In all but one case (Table III, case 7), mothers behaved nervously and showed distress (e.g., vocalizing, grinning, and attempts at infant retrieval). In Planckendael and Frankfurt, the targeted mothers frequently presented for G-G contacts to the female that had taken their infant.

## DISCUSSION

### **Interfering with Reproductive Cycles: Cycle Synchrony and Reproductive Inhibition**

We documented three case studies of possible female influence on other females' reproductive cycles: two apparent cases of menstrual synchrony and a possible case of reproductive inhibition in a low ranking female.

First, synchrony of the ovulatory cycle, possibly by way of chemical communication during G-G contacts [see Michael & Keverne, 1970], may have several selective benefits. Reproductive synchrony and overlap in timing of sexual activity of females in multimale- multifemale groups results in an operational sex ratio closer to 1 [Nunn, 1999a; Dixon, 1998, p 459], a condition that will decrease the monopolizability of multiple females by single males [Emlen & Oring, 1977; Nunn, 1999a]. This in turn may enhance opportunities for female choice. It has been suggested that a low potential for monopolization of females leads to a decreased risk of infanticide by males [van Schaik, 2000; Zinner & Deschner, 2000; Soltis et al., 2000]. Free-ranging bonobo groups approach an equal adult sex ratio [reviewed by Van Elsacker et al., 1995], and bonobo males have not been observed to monopolize females [Vervaecke, 1999; Kano, 1992; Stevens, 2000] or to commit infanticide [Kano, 1992]. We, thus, propose the hypothesis that the primary benefit of menstrual cycle synchrony in bonobos is to further decrease the monopolizability of females to males, thereby increasing the potential for female choice by dominant females and decreasing the likelihood of infanticide by males.

De Ridder's [2001] studies of bonobos at the Koln Zoo (Germany) suggest that control of ovarian cycles by the dominant female is likely to be a function of rank distance between females and that if a female has a small rank distance to the alpha female, she may escape ovarian control. In these situations, a female may benefit in

terms of access to mating partners by being fertile during the infertile part of the other females' cycles. De Ridder [2001] studied patterns of synchrony covering three cycles and found "antisynchrony" (alteration in timing leading to a pairwise shift) in menstrual cycles between the first and second-ranking females whereby these individuals exhibited fully complementary cycles. Both females were dominant over the males in the group and, as expected, the rank distance between the females was very low. Thus, the causes and consequences of cycle synchrony among bonobo females may be complex and dependent upon situational factors.

Finally, for high ranking females, the ultimate benefits of reproductive inhibition of lower ranking females may be similar to the benefits of interference with copulations and infanticide [see below: **reproductive potential hypothesis**: Niemeyer & Chamove, 1983; **sexual competition hypothesis**: Drukker et al., 1991; **resource competition hypothesis I**: Niemeyer & Anderson, 1983].

### **Interfering With Copulations**

It was striking that sexual interference of females resulted, in almost all cases, in termination of copulation. This is consistent with the **reproductive potential hypothesis** [Niemeyer & Chamove, 1983] or **sexual competition hypothesis** [Drukker et al., 1991]. Usually, interferences with copulations by females are less disruptive than interruptions by males, and sexual interruption is generally expressed by dominant males [Niemeyer & Anderson, 1983; Bruce & Estep, 1992]. The fact that in bonobos dominant females are capable of disrupting copulations and targeting other females aggressively during copulation confirms our premise that in this species female-female competition is less constrained by males. Alternative hypotheses that have been proposed with regard to the benefits of sexual interference [**protective hypothesis**: Gouzoules, 1974; **possessiveness of affiliative bonds**: Niemeyer & Chamove, 1983; **revanchism (revenge) hypothesis**: Nieuwenhuijsen et al., 1988; **dominance hypothesis**: Bruce, 1982; reviewed by Bruce & Estep, 1992] primarily explain mating harassment rather than mating interruption and are less applicable to the observed data.

Since female reproductive success is more limited by food than for males and since food can be directly converted to offspring [see Silk, 1993], resource competition might be considered a form of reproductive competition. The **resource competition I hypothesis** [Niemeyer & Anderson, 1983] may apply to female bonobos as well if their reproductive success is shown to be limited by resource use. This topic must be addressed by longitudinal studies in nature.

In order to escape sexual interference by higher-ranking females, a female may turn to various counterstrategies. First, she can attempt to copulate out of sight of these females. Low-ranking individuals of both bonobo study groups occasionally copulated out of sight of other group members [Vervaecke & Van Elsacker, 2000; Stevens, unpublished data]. A second counterstrategy may be the concealment of ovulation. If a female could lengthen her apparently fertile period, control of her sexual behavior by other females would become more difficult. Thus, theoretically, female bonobos can benefit by concealing ovulation from males, thereby decreasing monopolizability, and

from females by avoidance of copulation interference. This is expected to be significant for low-ranking females who are more likely to be targets of aggression by high-ranking females. High-ranking females receive very little aggression, and the costs of advertising ovulation should be lower for them. This hypothesis predicts that the reliability of the swelling as an ovulation advertisement is lower in lower ranking females.

In bonobos, copulations occur predominantly during the maximal swelling period which is only weakly linked with ovulation [Vervaecke, 1999]. This has been interpreted as concealing the moment of ovulation from males. Possibly, females benefit, also, by concealing ovulation from other females. We observed that, in Planckendael and Stuttgart, high-ranking females showed the most predictable swelling cycles. Low-ranking females in these groups had inter-menstrual intervals that were more variable and had less clearly delineated swelling periods, irrespective of age [Vervaecke et al., 1999b; Vervaecke, 1999]. In this way, ovulation in low-ranking females is more difficult to predict based on visual information. In the Planckendael group, the phase of the “supermaximal” genital swelling was most clearly linked to ovulation in the highest-ranking female but less so in the other females [Vervaecke, 1999; Heistermann et al., 1996]. Our sample size is, however, too limited to be conclusive, and the hypothesis remains to be tested.

#### **Interfering With Reproductive Output: Infant handling, Harassment, and Infanticide**

Possibly, the motivations of the perpetrators are ambiguous and several alternative non-exclusive hypotheses may be involved. The cases of infant harassment (Table III, cases 8 and 9) can be most parsimoniously explained as outright female reproductive competition and attempts at direct infanticide. Infants may be vulnerable to female infanticide only when their mother can be overpowered by more socially dominant females. In all cases observed, a higher ranking, adult female harassed the infant of a lower ranking, unrelated female.

Other cases of infant handling (Table III, cases 1-7) are more ambiguous. The fact that young, nulliparous females (Table III, cases 1 and 5) are involved conforms with Silk's [1999] predictions for the **learning to mother hypothesis**. In two cases, the perpetrator had lost an infant or fetus a few months before the incident, possibly explaining infant handling as a **by-product of selection for good maternal care** [Silk, 1999] (Table III, cases 4 and 6). Handling of infants by female bonobos other than the mother deserves further study to clarify the causes and consequences of these acts.

Theoretically, female bonding and coalitions are argued to represent counterstrategies that mothers may adopt against female aggression towards infants [Digby, 2000]. These behaviors are frequently observed in bonobos [Idani, 1991; Kano, 1992; Parish, 1993, 1996; Vervaecke et al., 2000; Parish & de Waal, 2000]. However, in the observed cases of infant harassment, there never occurred a subsequent act of support against the kidnapping female. Furthermore, bonobo coalitions are usually not directed against higher-ranking individuals [Vervaecke et al., 2000], and the perpetrators of the observed infant harassments were high-ranking females. Thus, it seems unlikely that female bonobos use bonding in this respect.



Figures 2a & b. Bonobo female relationships are characterized by both competition (a) as well as close affiliation (b). (Photos by Jeroen Stevens).

### CONCLUSIONS AND PROSPECTS

We expected to find a relatively clear expression of female intrasexual competition because bonobo females have the potential to dominate males. Based on several years of observation in a number of captive bonobo groups, we present anecdotal data that appear to confirm predictions from several theories about female sexual competition. In a species commonly considered egalitarian, competition appears to be a significant feature of female-female behavior and social organization (Figure 2).

Throughout evolution, the presence of and bonds with other females may have been advantageous selectively in terms of intersexual feeding benefits and protection from male harassment [Kano, 1992; de Waal, 2001]. However, once established, strong bonds set the stage for interindividual exploitation. Among free ranging bonobos, the costs to subordinates of competitive intra-female relationships are theoretically expected to be limited since females are free to migrate among groups. However, in practice, group movements may be constrained by multiple social or environmental factors [Dunbar, 1988]. Where group fissioning is extremely restricted and when resource competition intensifies, competition among females is expected to escalate, giving rise to “dear-enemy” relationships characterized by both aggression as well as close affiliation [Vervaecke, 1999]. The main problem concerning female sexual competition is the difficulty of quantifying the differential costs and benefits related to these acts in different environmental regimes. Benefits may be subtle, indirect, or postponed.

Besides the strategies we describe whereby females interfere with the reproduction of other females, other characteristics that may be sexually selected are also ex-

pressed in bonobos. Females show preferences for some males and do not copulate with all group males, despite promiscuous sexual mounts [Vervaecke, 1999]. The effects of rank on reproductive success in bonobo females also remains to be studied. Furthermore, the genital swelling in bonobo females is prominently visible during a large fraction of the menstrual cycle, apparently rendering these females more sexually attractive to males. We observed in a small sample of females (three groups, total of eight females) that swelling size could be related to rank [Vervaecke, 1999]. Whether genital swelling serves as a fitness indicator should be investigated [Pagel, 1994; Nunn, 1999b; Domb & Pagel, 2001; Dunbar, 2001].

In all investigated cases of female reproductive interference, dominant females seemed to exhibit greater potential than lower ranking individuals to interfere with other females' reproduction, a condition that may influence the apportionment of reproduction within female groups ("reproductive skew" [see Vehrencamp, 1983; Hager, this volume]). If lifetime reproductive success of dominant females is significantly higher than that of lower ranking females, as Pusey et al. [1997] demonstrated for chimpanzees, the interference strategies of dominant bonobo females may determine the apportionment of reproduction within a female group. Even low reproductive skew may have strong evolutionary consequences in great apes who display low lifetime breeding success due to slow maturation, relatively long interbirth intervals, and long reproductive life (approximately 32 years: De Lathouwers & Van Elsacker, unpublished data). De Lathouwers and Van Elsacker (unpublished data) calculated a theoretical reproductive output for captive bonobos of 0.19 infants per year, corresponding to Furuichi et al.'s [1998] estimated reproductive output of 0.18 infants per year for wild bonobo's. Therefore, the loss of every infant is costly, and investment in infants with regard to quality or sex of offspring can have significant future reproductive consequences.

Presently, more focused studies on specialized topics (e.g., mate choice, paternity, mating interference, attractivity, genital swelling cycles) in a larger number of captive groups are required, as well as additional field data on bonobo intra- and intersexual competition. Studies are needed that address how bonobo females gain and maintain their high social ranks and position themselves to influence other females' reproductive behavior. Such research can be conducted in captivity where adolescent females are exchanged between laboratories or zoos to mimic natural migration patterns.

Long term data on swelling and menstrual cycles can be gathered relatively easily, and the collection of urine and fecal samples allows for the non-invasive monitoring of ovarian activity and DNA analyses, both in the field as well as in laboratories and zoos [Heistermann et al., 1996; Gerloff et al. 1999]. Ideally, these data can be related to the hierarchical relationships and group dynamics discussed above. Related to this, female rank and interindividual rank distance can be useful tools in formulating predictions about menstrual synchrony and inhibition of ovulation. Additionally, the captive setting allows for controlled experiments on cycle synchrony induction.

Intra- and intersexual competition as well as female reproductive success should be measured in wild conditions. It is an unfortunate fact that continuing long-term research projects have not been feasible in the Congo, hampering the compilation of



longitudinal life history data or the documentation of rare events. Nonetheless, in each study undertaken, researchers should be sensitive to the diversity of female behaviors and the potential of female-female competition to increase the variance of lifetime reproductive success among members of this sex.

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#### REFERENCES

- Abbott DA. 1991. The social control of fertility. In: Box H, editor. Primate responses to environmental change. London: Chapman and Hall. p 75-89.
- Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349-368.
- Bowman LA, Dilley SR, Keverne EB. 1978. Suppression of oestrogen induced LH surge by social subordination in talapoin monkeys. *Nature* 275:56-58.
- Brereton AR. 1994. Return-benefit spite hypothesis: an explanation for sexual interference in stumptail macaques (*Macaca arctoides*). *Primates* 35:123-36.
- Bruce KE. 1982. Sexual harassment in a captive group of stumptail macaques. *Int J Primatol* 3:266.
- Bruce KE, Estep DQ. 1992. Interruption of and harassment during copulation by stumptail macaques, *Macaca arctoides*. *Anim Behav* 44:1029-1044.
- Bronson FH. 1989. Mammalian reproductive biology. Chicago: The University of Chicago Press.
- Charnov E, Berrigan D. 1993. Why do female primates have such long lifespans and so few babies? or Life in the slow lane. *Evol Anthropol* 1:191-194.
- Cunningham EJA, Birkhead TR. 1998. Sex roles and sexual selection. *Anim Behav* 56:1311-1321.
- De Ridder P. 2001. Reproductieve synchroniciteit bij bonobo's (*Pan paniscus*). Ph.D. Dissertation, University of Antwerp, Belgium.
- De Vleeschouwer K. 2000. Social organization, reproductive biology and parental care: an investigation into the social system of the golden-headed lion tamarin (*Leontopitecus chrysomelas*) in captivity. Ph.D. Dissertation, University of Antwerp, Belgium.
- De Vleeschouwer K, Leus K, Van Elsacker L. 2001. Multiple breeding females in captive

- groups of golden-headed lion tamarins (*Leontopithecus chrysomelas*): causes and consequences. *Folia Primatol* 72:1-10.
- de Waal FBM. 1987. Tension regulation and nonreproductive functions of sex in captive bonobos (*Pan paniscus*). *Nat Geog Res* 3:318-335.
- de Waal FBM. 2001. Apes from Venus: bonobos and human social evolution. In: De Waal FBM, editor. *Tree of origin*. Cambridge, MA: Harvard University Press. p 39-69.
- Digby L. 2000. Infanticide by female mammals: implications for the evolution of social systems. In: van Schaik C, Janson C, editors. *Infanticide by males and its implications*. Cambridge, UK: Cambridge University Press. p 423-446.
- Dixon AF. 1998. *Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings*. Oxford: Oxford University Press.
- Domb LG, Pagel M. 2001. Sexual swellings advertise female quality in baboons. *Nature* 410:204-206.
- Drukker B, Nieuwenhuijsen K, van der Werff ten Bosch JJ, Van Hooff JARAM, Slob AK. 1991. Harassment of sexual interactions among stump-tail macaques *Macaca arctoides*. *Anim Behav* 42:171-182.
- Dunbar RIM. 1980. Determinants and evolutionary consequences of dominance among female gelada baboons. *Behav Ecol Sociobiol* 7:253-265.
- Dunbar RIM. 1988. *Primate social systems*. London: Chapman and Hall.
- Dunbar RIM. 2001. What's in a baboon's behind? *Nature* 410:158.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197:215-223.
- Epple G, Katz Y. 1984. Social influences of estrogen excretion and ovarian cyclicity in saddle-back tamarins (*Saguinus fuscicollis*). *Am J Primatol* 6:215-227.
- Franz C. 1998. Female dominance and related behaviour patterns in bonobos (*Pan paniscus*). Ph.D. Dissertation, Karl-Franzens-Universität, Austria.
- Furuichi T. 1989. Social interactions and the life history of female *Pan paniscus* in Wamba Zaïre. *Int J Primatol* 10:173-197.
- Furuichi T, Idani G, Ihobe H, Kuroda S, Kitamura K, Mori A, Enomoto T, Okayasu N, Hashimoto C, Kano T. 1998. Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. *Int J Primatol* 19:1029-1043.
- Gerloff U, Hartung B, Fruth B, Hohmann G, Tautz D. 1999. Intra-community relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA-analysis of faecal samples. *Proc Royal Soc London B* 266:1189-1195.
- Gouzoules H. 1974. Harassment of sexual behavior in the stump-tail macaque *Macaca arctoides*. *Folia Primatol* 22:208-217.
- Harcourt AH. 1987. Dominance and fertility among female primates. *J Zool London* 213:471-487.
- Heistermann M, Möhle U, Vervaecke H, Van Elsacker L, Hodges K. 1996. Application of urinary and fecal steroid measurements for monitoring ovarian function and pregnancy in the bonobo (*Pan paniscus*) and evaluation of perineal swelling patterns in relation to endocrine events. *Biol Reprod* 55:844-853.

- Hohmann G, Gerloff U, Fruth B. 1999. Social bonds and genetic tests: kinship, association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour* 136:1219-1235.
- Hohmann G. 2001. Association and social interactions between strangers and residents in bonobos (*Pan paniscus*). *Primates* 42:91-99.
- Hrdy SB. 1974. Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol* 22:19-58.
- Hrdy SB. 1976. The care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Adv Stud Behav* 6:101-158.
- Hrdy SB. 1977. The langurs of Abu: female and male strategies of reproduction. Cambridge, MA: Harvard University Press.
- Hrdy SB. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1:13-40.
- Hrdy SB. 1981. The woman that never evolved. Cambridge, MA: Harvard University Press.
- Hrdy SB. 1984. Female reproductive strategies. In: Small MF, editor. Female primates: studies by women primatologists. New York: Alan R Liss Inc. p 103-109.
- Hrdy SB. 1999a. The woman that never evolved (2<sup>nd</sup> edition). Cambridge, MA: Harvard University Press.
- Hrdy SB. 1999b. Mother nature: a history of mothers, infants, and natural selection. New York: Pantheon Books.
- Idani G. 1991. Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatol* 57:83-95.
- Ims RA. 1990. The ecology and evolution of reproductive synchrony. *TREE* 5:135-140.
- Jones CB. 1986. Infant transfer behavior in humans: a note on the exploitation of young. *Aggressive Behavior* 12:167-173.
- Kano T. 1982. The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. *Primates* 23:171-188.
- Kano T. 1992. The last ape: pygmy chimpanzee behavior and ecology. Stanford, CA: Stanford University Press.
- Kano T. 1996. Male rank order and copulation rate in a unit-group of bonobos at Wamba, Zaïre. In: Mc Grew WC, Marchant LA, Nishida T, editors. Great ape societies. Cambridge, UK: Cambridge University Press. p 135-145.
- Kuester J, Paul A, Arnemann J. 1995. Age-related and individual differences of reproductive success in male and female Barbary macaques (*Macaca sylvanus*). *Primates* 36: 461-76.
- Kuester J, Paul A. 1996. Female-female competition and male mate choice in Barbary macaques (*Macaca sylvanus*). *Behaviour* 133:763-790.
- Leus K, Van Puijbroeck B. 2001. International studbook of the bonobo (*Pan paniscus*). Royal Zoological Society of Antwerp. ISIS Studbook Library CD-rom. Apple Valley, USA: International Species Inventory System
- McClintock MK. 1971. Menstrual synchrony and suppression. *Nature* 229:244-245.
- McClintock MK. 1981. Social control of the ovarian cycle and the function of estrous synchrony. *Amer Zool* 21:243-256.

- McClintock MK. 1983. Pheromonal regulation of the ovarian cycle: enhancement, suppression and synchrony. In: Vandenbergh JG, editor. Pheromones and reproduction in mammals. New York: Academic Press Inc. p 113-149.
- McClintock MK. 1984. Estrous synchrony: modulation of ovarian cycle length by female pheromones. *Physiol Behav* 32:701-705.
- Michael RP, Keverne EB. 1970. Primate pheromones of vaginal origin. *Nature* 225:84-85.
- Neugebauer W. 1980. The status and management of the Pygmy chimpanzee *Pan paniscus* in European zoos. *Int Zoo Yearbook* 64-70.
- Nicolson NA. 1987. Infants, mothers, and other females. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: The University of Chicago Press. p 330-342.
- Niemeyer CL, Anderson JR. 1983. Primate harassment of matings. *Ethol Sociobiol* 4:205-220.
- Niemeyer CL, Chamove AS. 1983. Motivation and harassment of matings in stump-tail macaques. *Behaviour* 87:298-323.
- Nieuwenhuisen K, Slob A.K, Van der Werff ten Bosch JJ. 1988. Gender-related behaviors in group-living stump-tail macaques. *Psychobiology* 16:357-371.
- Nunn CL. 1999a. The number of males in primate social groups: a comparative test of the socioecological model. *Beh Ecol Sociobiol* 46:1-13.
- Nunn CL. 1999b. The evolution of exaggerated swellings in primates and the graded-signal hypothesis. *Anim Behav* 58:229-246.
- Pagel M. 1994. The evolution of conspicuous oestrous advertisement in Old World monkeys. *Anim Behav* 47:1333-1341.
- Parish AR. 1993. Sex and food control in the "uncommon chimpanzee": how bonobo females overcome a phylogenetic legacy of male dominance. *Ethol Sociobiol* 15:157-179.
- Parish AR. 1996. Female relationships in bonobos (*Pan paniscus*). *Hum Nat* 7:61-96.
- Parish AR, de Waal FBM. 2000. The other "closest living relative": how bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and inter-sexual interactions, and hominid evolution. *Ann NY Acad Sci* 907:97-113.
- Pusey A, Williams J, Goodall J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277:828-831.
- Pusey A. 2001. Of genes and apes: chimpanzee social organization and reproduction. In: de Waal FBM, editor. *Tree of origin: what primate behavior can tell us about human social evolution*. Cambridge, MA: Harvard University Press. p 9-37.
- Robinson JG. 1982. Intrasexual competition and mate choice in primates. *Am J Primatol* 1:131-144.
- Savage A, Ziegler TE, Snowdon CT. 1988. Socio-sexual development, pair bond formation, and mechanisms of fertility suppression in female cotton-top tamarins (*Saguinus oedipus oedipus*). *Am J Primatol* 14:345-349.
- Silk JB. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *Am Nat* 21:56-66.
- Silk JB. 1993. The evolution of social conflict among female primates. In: Mason WA, Mendoza SP, editors. *Primate social conflict*. Albany: SUNY Press. p 49-84.

- Silk JB, Clark-Wheatley CB, Rodman PS, Samuels A. 1981. Differentiated reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). *Anim Behav* 29:1106-1120.
- Silk JB. 1999. Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Anim Behav* 57:1021-1032.
- Small MF. 1988. Female primate sexual behavior and conception: Are there really sperm to spare? *Current Anthropol* 29: 91-100.
- Smuts BB. 1987. Sexual competition and mate choice. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: The University of Chicago Press. p 385-399.
- Soltis J, Thomsen R, Matsubayashi K, Takenaka O. 2000. Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Beh Ecol Sociobiol* 48: 195-202.
- Sommer V. 1989. Sexual harassment in langur monkeys (*Presbytis entellus*): competition for ova, sperm, and nurture? *Ethology* 80:205-217.
- Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Beh Ecol Sociobiol* 41:291-309.
- Stern K, McClintock MK. 1998. Regulation of ovulation by human pheromones. *Nature* 392:177-179.
- Stevens J. 2000. Intraseksuele competitie en interseksuele strategieën bij mannelijke bonobo's (*Pan paniscus*) in gevangenschap. Ph.D. Dissertation. University of Antwerp, Belgium.
- Takahata Y, Ihobe H, Idani G. 1996. Comparing copulations of chimpanzees and bonobos: Do females exhibit proceptivity or receptivity? In: McGrew WC, Marchant LA, Nishida T, editors. *Great ape societies*. Cambridge, UK: Cambridge University Press. p 146-155.
- Thompson-Handler N, Malenky R, Reinartz G. 1995. Action plan for *Pan paniscus*: report on free ranging populations and proposals for their preservation. Milwaukee: Zoological Society of Milwaukee.
- Tutin CEG. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Beh Ecol Sociobiol* 6:29-38.
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. *Sexual selection and the descent of man 1871-1971*. Chicago: Aldine. p 136-179.
- Trivers RL. 1985. *Social evolution*. Menlo Park, CA: The Benjamin Cummings Publishing Company, Inc.
- Van Elsacker L, Vervaecke H, Verheyen R. 1995. A review of the terminology on aggregation patterns in pygmy chimpanzees (*Pan paniscus*). *Int J Primatol* 16:37-52.
- van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. *Comparative socioecology: the behavioural ecology of humans and other mammals*. Oxford: Blackwell. p 195-218.
- van Schaik CP. 2000. Social counterstrategies against infanticide by males in primates and other mammals. In: Kappeler PM, editor. *Primate males: causes and consequences of variation in group number*. Cambridge, UK: Cambridge University Press. p 34-52.

- Vehrencamp SL. 1983. A model for the evolution of despotic versus egalitarian societies. *Anim Behav* 31:667-682.
- Vervaecke H. 1999. Dominance relationships, bonding and the female genital swelling cycle in bonobos (*Pan paniscus*). Ph.D. Dissertation, University of Antwerp, Belgium.
- Vervaecke H, De Vries H, Van Elsacker L. 1999a. Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus*). *Int J Primatol* 21:47-68.
- Vervaecke H, Van Elsacker L, Heistermann M, Möhle U, Verheyen R. 1999b. Inter-menstrual intervals in captive bonobos (*Pan paniscus*). *Primates* 40:283-289.
- Vervaecke H, Van Elsacker L. 2000. Female sexual competition in a group of captive bonobos (*Pan paniscus*). *Primates* 41:109-115.
- Vervaecke H, De Vries H, Van Elsacker L. 2000. Distribution and function of coalitions in captive bonobos (*Pan paniscus*). *Primates* 41:247-263.
- Wallis J. 1985. Synchrony of estrous swellings in captive group-living chimpanzees (*Pan troglodytes*). *Int J Primatol* 6:335-350.
- Wallis J. 1992. Socioenvironmental effects on timing of first postpartum cycles in chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal F, editors. *Topics in primatology, volume 1: human origins*. Tokyo: University of Tokyo Press. p 119-130.
- Wallis J. 1994. Socioenvironmental effects on first full anogenital swellings in adolescent female chimpanzees. In: Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N, editors. *Current primatology volume II: social development, learning, and behavior*. Strasbourg, France: University of Louis Pasteur. p 25-32.
- Wallis J. 2002. Seasonal aspects of reproduction and sexual behavior in two chimpanzee populations: a comparison of Gombe (Tanzania) and Budongo (Uganda). In: Boesch C, Hohmann G, Marchant L, editors. *Behavioral diversity of chimpanzees and bonobos*. Cambridge (UK): Cambridge University Press. p 181-191.
- Wasser SK, Starling AK. 1988. Proximate and ultimate causation of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. *Am J Primatol* 16:97-121.
- Wasser SK. 1983. Reproductive competition and cooperation among female yellow baboons. In: Wasser SK, editor. *Social behavior of female vertebrates*. New York: Academic Press. p 349-390.
- Weller L, Weller B. 1997. Menstrual variability and the measurement of menstrual synchrony. *Psychoneuroendocrinology* 22:115-128.
- Weller L, Weller A, Koresh-Kamin H, Ben-Shosnan R. 1999. Menstrual synchrony in a sample of working women. *Psychoneuroendocrinology* 24:449-459.
- Wilson HC. 1992. A critical review of menstrual synchrony research. *Psychoneuroendocrinology* 17:536-546.
- Zinner D, Schwibbe MH, Kaumans W. 1994. Cycle synchrony and probability of conception in female hamadryas baboons *Papio hamadryas*. *Beh Ecol Sociobiol* 35:175-183.
- Zinner D, Deschner T. 2000. Sexual swellings in female hamadryas baboons after male take-overs: "deceptive" swellings as a possible female counter strategy against infanticide. *Am J Primatol* 52:157-168.

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