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## Sex differences in copulation attempts in wild bonobos at Wamba

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**Abstract** We examined sex differences in copulation attempts in a group of wild bonobos at Wamba, Congo, by analyzing the behavioral sequence. Most copulation attempts were initiated by approach or courtship behaviors by males. Males showed these behaviors when they were more than 5 m from females, whereas females did so only when males solicited them from within 5 m. Most copulations involved females showing perineal swelling, because males solicited those females more frequently and those females accepted copulation more frequently than did females in the non-swelling phase. Nevertheless, males solicited females in the non-swelling phase in one-third of copulation attempts, and those females accepted copulation in half of those attempts. This is markedly different from chimpanzees, in which sexual behaviors almost exclusively involve females in the swelling phase. The perineum of female bonobos during the non-swelling phase is soft and wrinkled but fairly large, which may attract males to some extent. The low, but existing, attractiveness and receptivity of female bonobos during the non-swelling phase might have evolved to control sexual competition among males and provide higher social status for females.

**Keywords** Bonobo · *Pan paniscus* · Sexual behavior · Perineal swelling · Sex difference · Wamba

### Introduction

Female bonobos spend a much greater proportion of their adulthood in estrus than do female chimpanzees (Wrangham 1993; Furuichi and Hashimoto 2002).

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However, recent studies have shown that compared with female chimpanzees, female bonobos show fewer positive behaviors toward copulation and have a lower copulation rate during estrus (Takahata et al. 1996; Furuichi and Hashimoto 2002; Wrangham 2002). These differences may influence the benefits that females gain by copulating with many males or with the best males, and by reducing the time required to achieve pregnancy.

To discuss these points further, we need to evaluate the sexual attractiveness, receptivity, and proceptivity of females in wild groups (Beach 1976). Of these, proceptivity is usually measured by the frequency with which females initiate interactions that lead to copulation. However, the definition of initiation behavior differs among studies. It is especially difficult to confirm the first approach in an interaction in the field, and whether the first approach is taken as an initiation behavior may generate different results with regard to which sex initiates copulation attempts (Kano 1989). We designed this study to enable detailed observation of behavior starting from the first approach. We examined the roles of males and females in the copulation attempts, and differences in male and female sexual behaviors according to whether females were in the swelling or non-swelling phases.

### Methods

We observed the E1 group of wild bonobos living at Wamba, Democratic Republic of Congo (Kano 1992) for 43 days between 29 December 1990 and 26 February 1991. The E1 group consisted of 29 individuals, including 6 adult males and 9 adult females (Hashimoto 1997).

The group visited two permanent and other temporary provisioning sites in the forest. Data for this study were collected only at these sites, which afforded good visibility for observation. We scanned the behaviors of all individuals within sight at short intervals to confirm behaviors that initiated interactions leading to copulation.

We recorded the sequence of behavioral interactions between adult males and adult females that involved courtship behaviors and/or copulation; we called these sequences “copulation attempts.” Those that did or did not result in copulation were called “successful copulation attempts” or “unsuccessful copulation

attempts,” respectively. Approach behaviors included a participant walking toward or following another. Courtship behaviors included swaying the upper body backward, standing bipedally, raising the arms, touching the other with the hands or penis, leading the other by walking away while looking back, dropping or shaking branches, and presenting (Kuroda 1984; Kano 1989, 1997). We assumed that a copulation attempt ended when the behavioral sequence ceased for more than 1 min. Some copulation attempts involved two or more episodes of copulation. We recorded the distance (less than 1 m or more than 1, 3, or 5 m) between the participants when each behavior was performed.

The state of perineal swelling of each female was recorded on each day of observation. The degree of swelling was evaluated by firmness as follows: a turgid, lustrous perineum lacking fine wrinkles on the surface (firmness level 3), a somewhat soft perineum with fine wrinkles (firmness level 2), or a very wrinkled perineum that swayed during walking (firmness level 1) (Furuichi 1987). The firmness-3 period is comparable with the maximal swelling period of bonobos in other studies (e.g., Dahl 1986; Kano 1992), and of chimpanzees (e.g., Graham 1981; Hasegawa and Hiraiwa-Hasegawa 1983). Previous field studies have shown that most bonobo copulations occur with females during the maximal swelling period (Furuichi 1987, 1992; Kano 1992; Takahata et al. 1996), and laboratory studies have shown that female bonobos most probably ovulate in the latter half of this period (Heistermann et al. 1996; Reichert et al., 2002). In this article, the firmness-3 period is called the “swelling phase,” whereas the firmness-2 and firmness-1 periods constitute the “non-swelling phase.”

## Results

We observed 53 copulation attempts. They involved five of six adult males, and there was no significant relationship between the frequency of copulation attempts and the rank order of males. They also involved six of nine adult females. Two of the three females for whom copulation was not observed had infants less than 1 year old. Since there were too few observations of complete interactions to analyze differences among individuals, all cases were pooled for the following analyses.

The initiation behavior was observed for 32 copulation attempts, which included 23 successful and 9

unsuccessful attempts (Table 1). We defined “initiation behavior” as a behavior that was performed by the first participant to act in a copulation attempt. The initiation behavior was either an approach (if the two participants were apart) or a closer approach or courtship behavior (if the participants were already near one another). Males showed the initiation behavior in 22 of the 23 successful copulation attempts and in all 9 unsuccessful copulation attempts. Male initiation of successful copulation attempts was followed by female approaching, leading, and presenting, but females did not approach or perform courtship behaviors during unsuccessful copulation attempts. There was no forced copulation, and no copulation attempts ended unsuccessfully due to intervention by other adult males during this study. Therefore, female response determined, in the main, the results of copulation attempts.

In copulation attempts, males began to show approach or courtship behaviors at a distance greater than that observed for females (Fig. 1). Unlike the “initiation behavior” described above, the “first behaviors” here were those performed by both the male and female, regardless of which initiated the attempt. Whereas males sometimes performed an approach as the first behavior when females were more than 5 m apart from them, females performed an approach only when males were within 5 m. Whereas males performed a courtship behavior as the first behavior when females were within 5 m, females performed it only when males were within 1 m.

The number of successful and unsuccessful copulation attempts with respect to the swelling and non-swelling phases were compared (Table 2). If corrected for the observed number of female days per phase, copulation attempts tended to occur more frequently for females in the swelling phase than for those in the non-swelling phase. Copulation attempts were also more frequently successful with females in the swelling phase,

**Table 1** Behaviors observed during copulation attempts

Copulation attempts	Sex	Approach	Courtship behaviors							
			All types	Present	Sway back	Bipedal stand	Raise arms	Touch body	Lead	Drop or shake branches
Successful attempts ( <i>n</i> = 23)										
Initiation behaviors	Male	12	10		7	6	1	1		1
	Female	1	0							
All behaviors <sup>a</sup>	Male	21	39		21	17	3	3	3	3
	Female	14	20	19					1	
Unsuccessful attempts ( <i>n</i> = 9)										
Initiation behaviors	Male	3	6		5	2	1			
	Female	0	0							
All behaviors <sup>a</sup>	Male	5	20		12	8	4	4	2	
	Female	0	0							
All attempts ( <i>n</i> = 32)										
Initiation behaviors	Male	15	16		12	8	2	1		1
	Female	1	0							
All behaviors <sup>a</sup>	Male	26	59		33	25	7	7	5	3
	Female	14	20	19					1	

<sup>a</sup> All behaviors observed throughout the copulation attempts, including the initiation behavior

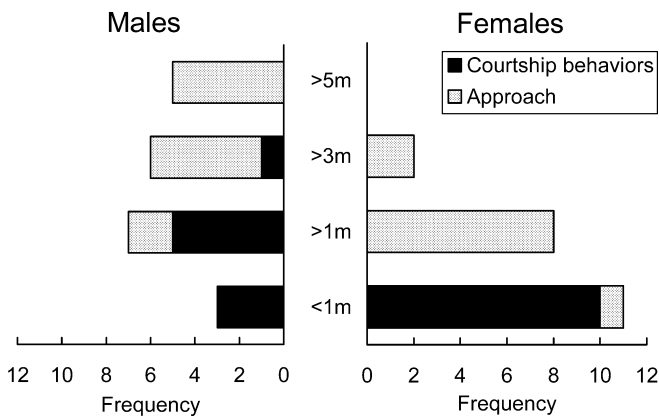
and therefore females copulated more frequently during the swelling phase. Interestingly, however, 11 of 31 copulation attempts initiated by males involved females in the non-swelling phase and females accepted 5 of these attempts.

## Discussion

This study found that male bonobos were almost exclusively the active participant in copulation attempts, whereas females did not show apparent proceptivity. Males initiated 97% of copulation attempts by approaching or performing courtship behaviors. During copulation attempts, males exhibited these behaviors more frequently, and from a greater distance, than did females. By contrast, copulation attempts were successful only when females reacted positively.

Previous studies of wild bonobos also showed that males initiate copulation more often than females. Males' approach or courtship behaviors initiated 71% (Kano 1989), 74% (Kano 1992), and 97% (Furuichi 1992) of copulations for which the initiator was known. Takahata et al. (1996) observed an approach or display by a male in 89% of copulations, although it was not necessarily the initiation behavior.

For chimpanzees, Goodall (1986) reported that adult males typically initiated copulation at Gombe. At Mahale, males initiated 58% of copulations (Nishida 1980) and 84% of copulation attempts (Nishida 1997).



**Fig. 1** Distance at which individuals performed the first behaviors in each copulation attempt. Three cases were excluded (one courtship behavior by a male and two approaches by females) because the distance was not recorded. Four approaches by males classified here as occurring more than 3 m away might have been more than 5 m away

However, initiation in these studies did not include approaches. Conversely, Takahata et al. (1996) showed that females demonstrated approach and courtship behaviors more frequently than did male chimpanzees at Mahale, and our unpublished data suggest that copulation attempts are initiated by approach behaviors on the part of females more frequently in chimpanzees in the Kalinzu Forest than in bonobos at Wamba. To evaluate the differences in male and female proceptivity between chimpanzees and bonobos more precisely, we need to conduct comparative studies using a consistent definition of initiation behavior that takes into consideration the first approach. Although it depends on the visibility at the study sites, it should at least be possible to confirm all approaches occurring within 10–20 m of estrous females.

This and previous studies all indicate that in bonobos the majority of copulations occur during the swelling phase (67–82%, this study; Furuichi 1987, 1992; Kano 1989; Takahata et al. 1996). These results can be explained by the finding that males attempted copulation more often with females in the swelling phase, and females accepted copulation attempts more often while in the swelling phase. However, males directed one-third of all copulation attempts to females in the non-swelling phase, and females accepted half of those attempts. This situation differs from that of chimpanzees, in which copulation attempts or copulations almost exclusively involve females in the maximal swelling phase (94–99%, Hasegawa and Hiraiwa-Hasegawa 1983; Goodall 1986; Takahata et al. 1996; Nishida 1997).

These data suggest that female bonobos are attractive and receptive, to some extent, during the non-swelling phase. In female chimpanzees, cyclic changes in the firmness and size of the perineum occur together, with the perineum shrinking completely during the non-swelling phase. In female bonobos, however, the swelling cycle is distinctive in terms of the firmness of the perineum, whereas the size of the perineum does not change much throughout the menstrual cycle (Furuichi 1987; Heistermann et al. 1996). The size of the perineum in bonobos depends on female age: the perineum of fully adult females is of medium size even during the non-swelling phase, and the perineum of young adult females is small, but visible, throughout the swelling cycle. Male bonobos may be more or less attracted to a visible perineum even if it is soft and wrinkled and may consequently solicit such females for copulation.

Previous studies suggested that the prolonged estrus of female bonobos allows females to attend a mixed

**Table 2** Comparison of copulation attempts during the swelling and non-swelling phases

Phase	Firmness level	Female days per phase	Copulation attempts		
			All cases	Successful	Unsuccessful
Swelling	3	176	21	18	3
Non-swelling	2	70	8	3	5
	1	139	3	2	1

party irrespective of estrous state. Due to the lowered estrous sex ratio (number of adult males per estrous female) in bonobos, competition among males is controlled and agonistic interactions involving estrous females occur only rarely. The high social status for females may also be related to the prolonged attractiveness of females (White 1988; Furuichi 1989, 1997; Kano 1989, 1992; Wrangham 1993, 2002; Furuichi and Hashimoto 2002). Female bonobos may also have evolved some degree of sexual attractiveness and receptivity during the anestrus non-swelling phase, which may bring about effects on the group life of females that are similar to those brought about by prolonged estrus.

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