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ORIGINAL ARTICLE

Chie Hashimoto · Takeshi Furuichi

Comparison of behavioral sequence of copulation between chimpanzees and bonobos

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Abstract We compared sex differences in behaviors leading to copulation of chimpanzees (*Pan troglodytes*) in the Kalinzu Forest, Uganda with those of bonobos (*Pan paniscus*) at Wamba, D.R. Congo, using the same definition. Female chimpanzees were more likely to initiate copulation than female bonobos. While most of copulations (96%) were initiated by males in bonobos, among chimpanzees only 63% of copulations were initiated by males. Female bonobos initiated an interaction leading to copulation when males approached them within a short distance. On the other hand, both male and female chimpanzees initiated behavior at a longer distance. Higher proceptivity and a higher copulation rate during the maximal swelling period of female chimpanzees might suggest that they gain greater benefits from a high frequency of copulations than do female bonobos.

Keywords Copulation · *Pan troglodytes* · *Pan paniscus* · Proceptivity · Sex differences

Introduction

Because female bonobos (*Pan paniscus*) spend a much greater proportion of their adulthood in estrus than do female chimpanzees (*Pan troglodytes*) (27% for bonobos vs 4.2–6.4% for chimpanzees, Furuichi and Hashimoto 2002), female bonobos may experience a higher number of copulations throughout a lifetime than do female chimpanzees (Wrangham 1993; Furuichi and Hashimoto 2002). However, recent studies showed that female chimpanzees have a higher copulation rate during estrus than do female bonobos, and that female bonobos show lower proceptivity toward copulation than do female chimpanzees (Furuichi and Hashimoto 2002, 2004; Wrangham 2002; Hashimoto and Furuichi 2003).

Previous studies reported that most copulations were initiated by approach or courtship behaviors of males in bonobos (Kano 1989, 1992; Furuichi 1992; Takahata et al. 1996; Furuichi and Hashimoto 2004). For chimpanzees, on the other hand, results differ among studies. Adult males in Gombe are reported to initiate copulation interactions although sex differences have not yet been determined (Goodall 1986). In Mahale, males initiated 58% of copulations (Nishida 1980) and 84% of copulation attempts (Nishida 1997), and females showed approach or solicitation in copulation interactions more frequently than males did (Takahata et al. 1996). These studies used different definitions for initiation of copulation: Goodall (1986) and Nishida (1997) did not take a first approach as an initiation behavior while Takahata et al. (1996) did. Therefore, it is difficult to tell which sex initiates copulation interactions in chimpanzees and what is different between chimpanzees and bonobos. In this study, we conducted a research on chimpanzees in the Kalinzu Forest, Uganda, using the same definition as our previous study on bonobos: we recorded approaches that started at a distance more than 5 m, and included the first approach in the initiation behaviors (Furuichi and Hashimoto 2004).

Females of chimpanzee and bonobo copulate several hundred times for one conception, and there have been many theories proposed to explain such a high number of copulations (Boesch and Boesch-Achermann 2000; Wrangham 2002). The "best male" hypothesis supposes that frequent copulation would benefit females from finding the best males or genes by making males compete with each other (e.g., Short 1979; Dixson 1998). In the "many male" and "social

C. Hashimoto (✉)
Primate Research Institute, Kyoto University,
Kanrin, Inuyama Aichi, 484-8506, Japan
E-mail: hashimot@pri.kyoto-u.ac.jp
Tel.: +81-568-630540
Fax: +81-568-630085

T. Furuichi
Faculty of International Studies, Meiji-Gakuin University,
Tokyo, Japan

passport'' hypotheses, females may be able to expect various kinds of service from the mates, including food supply, support in the agonistic interactions, and paternal care for the infant (e.g., Hrdy 1981; Whitten 1987; Wright 1990; Boesch and Boesch-Achermann 2000). In the ''paternity confusion'' hypothesis, females may be able to confuse males about paternity of offspring by copulating with many males and prevent infanticide by males (e.g., Hrdy 1977; van Schaik 2000). In the ''optimal period for producing next offspring'' hypothesis, females of a species with the shorter optimal period, such as chimpanzees compared with bonobos, may show more proceptive behaviors toward copulations (Furuichi and Hashimoto 2002; Wrangham 2002). Though these hypotheses have not been fully verified quantitatively, all of them suppose that the high frequency of copulations would lead to benefit for females. If this is the case, female chimpanzees that perform copulations at a higher frequency during the estrous period may exhibit higher level of proceptivity. Therefore, this study to compare behaviors leading to copulation between males and female, and between chimpanzees and bonobos, will provide an insight into female reproductive strategies of these species.

Methods

Study site and animals

We observed the M group of wild chimpanzees living in the Kalinzu Forest Reserve, which is located in western Uganda 30°07′E, 0°17′S) at 1,200–1,500 m above sea level (Howard 1991; Hashimoto 1995; Hashimoto et al. 2001). This forest is classified as a medium altitude moist evergreen forest (Howard 1991). Annual rainfall from June 1997 to May 1998 was 1,584 mm (Hashimoto et al. 1999).

Observations were conducted over 11 months in July–October 2001, August–November 2002, and August–October 2003. During these study periods, we identified all 20 adult male members of the group. However, we identified only a subset of adult female (17) and immature (13) members, because anoestrous females with dependent offspring tended to range independently and were rarely observed in a mixed sex party on which most of observations were made.

We observed the E1 group of wild bonobos living at Wamba, Democratic Republic of Congo (0°02′N, 22°35′E). The temperature of this area is fairly stable throughout the year, with a mean daily temperature of around 24°C. Annual rainfall is about 2,000 mm. The study site is located in the lowland tropical forest. Further details are available elsewhere (Kano 1992; Hashimoto et al. 1998). Observation was made for 43 days between December 1990 and February 1991 (Furuichi and Hashimoto 2004). We observed 29 individuals of the E1 group, including six adult males and nine adult females, during the study period (Hashimoto 1997).

Observations and definitions

For bonobos at Wamba, we made our observations at artificial provisioning sites that afforded good visibility for observations. We recorded the behaviors of all individuals within sight at short intervals to identify behaviors leading to copulation (Furuichi and Hashimoto 2004). For chimpanzees in the Kalinzu Forest, we followed an estrous female using the focal animal sampling method. We recorded all behaviors of the focal animal and ''copulation interactions'' that were defined as follows:

- We called a sequence of behavioral interactions between adult males and adult females that involved copulation a ''copulation interactions.'' A copulation interaction started when either of the participants performed an approach or courtship behaviors. We assumed that the copulation interaction was interrupted or ended when either of the participants started feeding, grooming, or social interactions with animals other than the partner, or when the behavioral sequence ceased for more than 1 min. Some copulation attempts involved two or more episodes of copulations if those copulations occurred at intervals less than one minute. Unlike ''copulation attempt'' of Furuichi and Hashimoto (2004), copulation interactions in this paper include only the interactions that successfully ended in copulation.
- For both chimpanzees and bonobos, we analyzed only complete behavioral sequences, i.e., those that were observed from the first initiating behavior to the completion of copulation. When an interaction leading to copulation occurred, we recorded the distance between participants (less than 1 m or more than 1, 3, or 5 m) at which each behavior was started.
- We defined ''initiation behavior'' as the behavior that was performed by the first participant to act in a copulation interaction. The initiation behavior was either an approach or a courtship behavior. Courtship behaviors included ''present'', ''sway back'', ''bipedal stand'', ''raise arms'', ''touch body'', ''lead'', ''drop or shake branches'' (Furuichi and Hashimoto 2004).
- We also defined the ''first behavior'' in a copulation interaction. Unlike the ''initiation behavior'', the ''first behavior'' applied to the behavior that was performed in the first by a male and a female, respectively, regardless of which sex initiated the copulation interaction (Furuichi and Hashimoto 2004). Therefore, all copulation interactions had two first behaviors: one performed by a male and another performed by a female. We classified the first

behaviors into four categories: approach, courtship behavior, copulation, and others (e.g., pant grunt in chimpanzees).
– We recorded the state of perineal swelling for adult females each time they were observed. A female was considered to be in a maximal swelling period, or estrus, when her perineum appeared turgid and lustrous and lacked fine wrinkles on its surface (Furuichi 1987; Furuichi and Hashimoto 2004).

Results

We observed 674 copulation interactions of chimpanzees in the Kalinzu Forest, of which 274 interactions were complete. On the other hand, we observed 36 copulation interactions of bonobos at Wamba, and we could observe all behaviors for 23 of these interactions (Furuichi and Hashimoto 2004).

First, we compared initiation behaviors between chimpanzees and bonobos. In bonobos, females rarely performed initiation behaviors in copulation interactions (one of 23 cases, Fig. 1). The proportion of initiation was significantly higher for males than for females (Mann–Whitney U-test, $n_{male} = 4$, $n_{female} = 5$, $U = 0.0$, $p < 0.01$). By contrast, among chimpanzees, females performed initiation behaviors in considerable numbers of copulation interactions (106 of 274 cases), though the proportion of initiation was significantly higher for males than for females (Mann–Whitney U-test, $n_{male} = 20$, $n_{female} = 7$, $U = 30.5$, $p < 0.05$). If we compare using individual females as the unit of analysis, female chimpanzees initiated copulation interactions significantly more frequently than did bonobo females (Mann–Whitney U-test, $n_{chimpanzee} = 7$, $n_{bonobo} = 5$, $U = 0.0$, $p < 0.01$). In bonobos, initiation behaviors included similar proportions of approach and courtship behaviors, while in chimpanzees, initiation behaviors included more approaches than courtship behaviors.

Second, we compared first behaviors between bonobos and chimpanzees. In bonobos, females performed their first behavior after males had approached her to a short distance (mostly less than 3 m; Fig. 2). The proportion of the first behaviors that were performed at a distance > 3 m was higher for males than for females, though statistically non-significant due to the small sample size (Mann–Whitney U-test, $n_{male} = 4$, $n_{female} = 5$, $U = 3.0$, $p = 0.06$). On the other hand, in chimpanzees, both males and females often performed the first behavior at a longer distance, without an apparent sex difference (Mann–Whitney U-test, $n_{male} = 20$, $n_{female} = 7$, $U = 49.5$, $p = 0.26$). In comparison between species, the proportion of the first behaviors that were performed at a distance > 3 m was higher for female chimpanzees than for female bonobos (Mann–Whitney U-test, $n_{chimpanzee} = 7$, $n_{bonobo} = 5$, $U = 1.0$, $p < 0.01$).

In some cases, male and female chimpanzees were grooming each other or staying within a short distance after the copulation, and they copulated again after a while. In such cases, the first behavior of the second copulation sequence was "copulation" for the male and "present" for the female.

Discussion

Although previous studies reported which sex initiated copulation in chimpanzees and bonobos (bonobos: Kano 1989, 1992; Furuichi 1992; Takahata et al. 1996; Furuichi and Hasihmoto 2002, 2004; chimpanzees: Goodall 1986; Takahata et al. 1996; Nishida 1980, 1997), it was difficult to make interspecies or inter-site comparisons because of differences in definitions. For instance, some studies considered the first approach as the initiation of copulation (Goodall 1986; Nishida 1997) while others did not (Takahata et al. 1996). In this

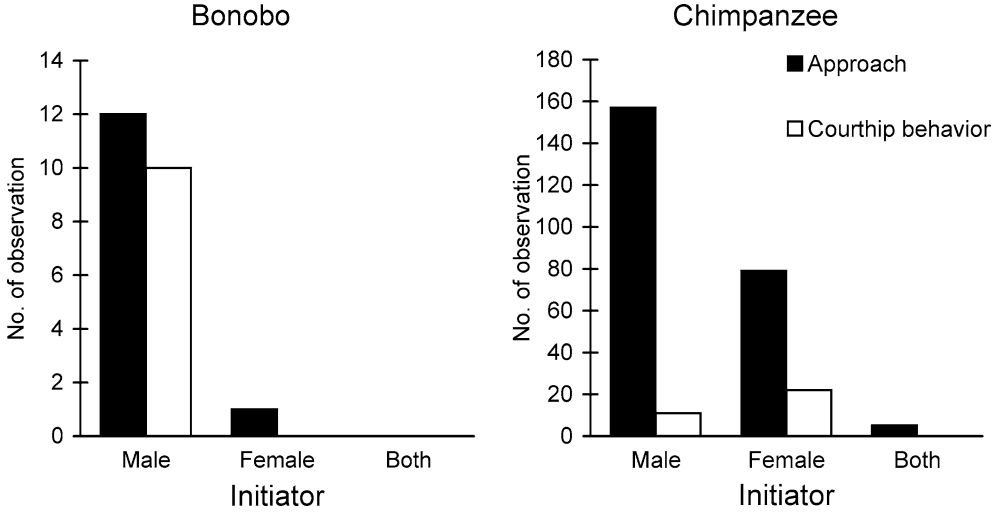

Fig. 1 Sex of the initiator of copulation interactions. For bonobos, we used data from Fig. 1 of Furuichi and Hashimoto 2004

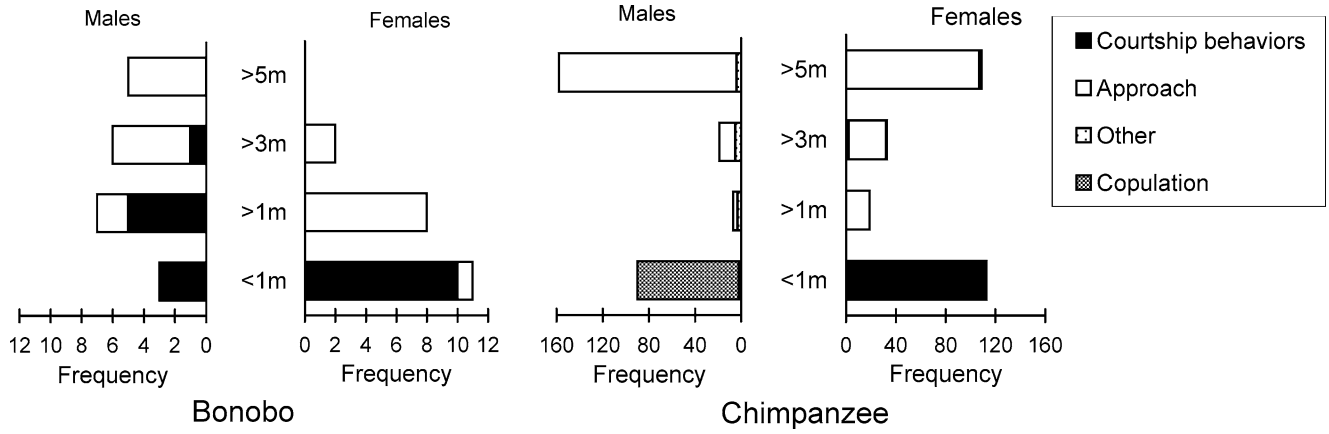

Fig. 2 Distance at which individuals performed the first behaviors in each copulation interactions. For bonobos, we used data from Fig. 1 of Furuichi and Hashimoto 2004

study, we used the same definition to compare copulation interactions in chimpanzees and bonobos and revealed the roles that each sex played in copulation interactions in each species.

As all previous studies showed, male bonobos played a more active role in copulation than females did. Males initiated most copulation interactions and females waited for males to approach them in most copulation interactions. After males approached females to a short distance, females approached males or presented.

On the other hand, female chimpanzees played a more active role in copulation interactions than female bonobos did. As all previous studies (Goodall 1986; Nishida 1997), this study showed that male chimpanzees initiated more copulation interactions than female chimpanzees did. However, unlike bonobos, female chimpanzees showed initiation behaviors in 39% of copulation interactions, and they showed first behaviors at a greater distance than female bonobos did.

Proceptivity of female chimpanzees toward copulation might explain the high frequency of copulation. If we consider the frequency of copulation for only during the maximal swelling period, female chimpanzees mate at higher frequencies than female bonobos do (Furuichi and Hashimoto 2002). Female chimpanzees of our study group show a particularly high copulation rate. They copulated 2.93 times/h during this study (Hashimoto and Furuichi 2003), which was much higher than the copulation rate for bonobos of 0.11 times/h during this study period, and 0.37 times/h during our 1985–86 study (Furuichi and Hashimoto 2002). Female chimpanzees looked for the next partner of copulation just after they had finished the first copulation. They often left the first copulation partner where he was resting, and moved toward the next adult male who was waiting for her. Such an active movement of females contributed to shortening the interval of copulations.

The fact that female chimpanzees show a higher proceptivity and copulate at a higher rate may suggest that female chimpanzees gain greater benefits from a high frequency of copulations than do female bonobos. Such interspecies differences may provide a key to examine hypotheses that have been proposed to explain the high frequency of copulations of chimpanzees and bonobos, including "many male" "social passport" "best male" "paternity confusion", and "optimal period for producing next offspring" hypotheses (Whitten, 1979; Short, 1979; Hrdy 1981; Wright 1990; Dixson 1998; Boesch and Boesch-Achermann 2000; Furuichi and Hashimoto 2002; Wrangham 2002).

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