Mechanisms and socio-sexual functions of female sexual swelling, and male mating strategies in wild bonobos

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My PhD research focused on the mechanisms and socio-sexual functions of sexual swelling in wild female bonobos. The sexual swellings of Old World monkeys, chimpanzees and bonobos are exaggerated in size and color. They influence male behavior by indicating ovulation probability, and they play an important role in multi-male/multi-female primate societies. Sexual swellings of female bonobos are known to have deviated the most among species that exhibit sexual swellings; for example, the reliability of signaling the probability of ovulation might be the lowest. Female bonobos also resume sexual swelling much earlier after parturition when compared with female chimpanzees, and they sometimes exhibit very long periods of maximal swelling that continue for over a month. How and why were these characteristics of sexual swellings of female bonobos achieved, and how do males deal with the poor reliability of the signal? This dissertation aimed to answer these questions.

In Chapter 2, I examined the dynamics of urinary metabolites of steroid sex hormones (urinary estrone conjugate; E1C and pregnanediol glucuronide; PdG), and the changes in reproductive parameters (length and interval of maximal swelling phase) in relation to time after parturition. Results confirm that a rise in urinary E1C coincided with the onset of the maximal swelling phase. I also confirmed that a constant increase of PdG, probably from the corpus luteum, above the baseline after ovulation coincided with detumescence of the maximal swelling. Lactation and early loss of pregnancy probably influence the considerable variation in length of the maximal swelling phase within an individual and between individuals. Female bonobos resume maximal swelling cycles on average 240.5 days after parturition, although females normally do not get pregnant until 3 years later. This early resumption of sexual swelling seems to be a unique feature of female bonobo sexual swellings, and might perform some regulative function in male mating competition by allowing males more mating opportunities. These results indicate that female bonobos appear

to require approximately 3 years to recover physically after lightening the energy burden of lactation, similar to female chimpanzees. However, female bonobos resume maximal swelling much earlier than female chimpanzees do. Female bonobos may resume maximal swelling even at lower levels of estrogen for social purposes, such as to reduce male sexual competition, to increase the social status of females, and to develop close female associations even when they are not yet ready for conception.

In Chapter 3, I tested the hypothesis that males can cope with the poor predictability of ovulation and can determine ovulatory phase. Results support the predictions of the "males know" hypothesis: bonobo males selectively followed females who had a higher probability of ovulation. In particular, male rank predicted an increase in the number of copulations with the female with the highest probability of ovulation. High-ranking males also engaged in agonistic interactions more often when they intensively followed a given female. When there were several females with maximal swellings, group males were more likely to follow females with older dependent offspring, and whose maximal swelling phase was close to detumescence. This suggests that even though the predictability of ovulation of this study population is poor, they can cope with this poor signal by adopting simple rules. It is also possible that males have the ability to discriminate ovulation more precisely using the subtle changes in color or size of swellings as well as other behavioral or olfactory cues. To test this possibility, we need to take more precise measurements of sexual swellings using digital photography.

In Chapter 4, I proposed a hypothesis that sexual swelling in female bonobos increases their attractiveness to other females and thereby facilitates affiliative social interaction with them. I found that free-ranging female bonobos with maximal sexual swelling engaged in affiliative social interactions with other females, including genito-genital rubbing, staying in close proximity and grooming, more frequently than females without maximal swelling. These tendencies suggest that females with maximal swelling were attractive to other females. The results also suggest that the benefits of maximal swelling might vary among females depending on their life-history stage. In particular, young females may benefit more from prolonged maximal swelling through increased grooming reciprocity and staying in close proximity to other females. Thus, the results support the hypothesis that one function of prolonged maximal swelling in bonobos is to increase female

attractiveness to other females, thereby enhancing affiliative relationships between females in a male-philopatric social system. Females with maximal swelling probably increase attractiveness to both males and females, and this might allow those females to benefit from group living. Though I do not propose the evolutionary mechanism in this study, it is possible that signals from sexual swellings influence other females' attitudes toward females with maximal swelling. Given that the sexual swelling is a very important body part, and the cost of signaling using that vulnerable body part is high, sexual swelling can serve as an honest signal to evaluate another's motivation or the relationship between two individuals.

Lastly, although the early resumption of sexual swelling might have a regulatory role in male mating competition to some extent, this study showed that male mating competition prevails in bonobos, and that male rank is an important factor in reproductive success, as has been found in chimpanzees. As shown in Chapter 3, male bonobos allocate their mating efforts based on variations in the sexual swelling of females. If male bonobos can precisely extrapolate ovulation probability, as males can in the other species that exhibit sexual swelling, it would be difficult to maintain the argument that milder male–male competition for reproduction in bonobos is explained by a poor predictability of ovulation. The high social status (or balanced power distribution) of female bonobos can influence male mating competition, as the high social status of females might allow female choice to exert influence on males' reproductive success. If that is the case, then less restriction on copulation opportunities for lower-ranking males may also be due to female choice. Therefore, in future research, it will be important to investigate how female bonobos can achieve high social status in their society, as well as the socio-regulatory role of prolonged receptivity of female bonobos. This will allow us to evaluate whether the hyper-sexuality of bonobos results in the peaceful bonobo society, or whether hyper-sexuality is itself a result of more balanced power distribution between the sexes.