

**A comparative study of male–male relationships in chimpanzees (*Pan troglodytes*)
and bonobos (*P. paniscus*)**

Digest

Chapter 1 General Introduction

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are known for their grouping patterns. Although both species have fission–fusion dynamics as a common basis, the stabilities of their temporary parties are largely different. Chimpanzees form parties that vary in size and members, while bonobos form large and stable parties which include most party members. These two species are also largely different from each other in terms of male aggression. While male chimpanzees frequently show severe aggressive behaviors in various contexts, aggression among male bonobos is much less intense. The difference in grouping patterns might be related to the difference in their male aggression. This study aims to evaluate the similarities and differences in male–male relationships between chimpanzees and bonobos from the perspective of avoiding the disadvantages caused by male aggression. Exploring the factors shaping the differences in male aggression and the grouping patterns between the two species might provide cues for understanding the evolution of male-philopatric societies.

Chapter 2

Methods: Observations on male chimpanzees were conducted at Kalinzu Forest Reserve, Uganda, and the relationship between male dominance rank and party participation in male chimpanzees was evaluated.

Results and discussion: I found that low-ranking males spent more time alone than other males when

females with MS were absent. In contrast, when females with MS were present, males of all ranks showed a similar tendency of party attendance. I also found that the aggressive interactions increased with the number of males irrespective of the presence or absence of females with MS, and low-ranking males attracted aggression more frequently than higher-ranking males. These results suggest that low-ranking males frequently range alone to avoid aggression from other males unless they attend parties to seek mating opportunities. I conclude that the fission–fusion dynamics offer alternative tactics for low-ranking males to mitigate the costs of these disadvantages when competing for survival and reproduction against other adult males.

Chapter 3

Methods: Observations on male bonobos were conducted at Wamba, Democratic Republic of the Congo, and the party attendance and aggressive interactions among males were investigated. The intermale relationships of bonobos at Wamba and chimpanzees at Kalinzu were compared to discuss the similarities and differences in male–male relationships between the two species and to identify the factors responsible for these differences.

Results and discussion: Male bonobos did not show the tendencies of a high degree of dispersion that male chimpanzees showed in the absence of receptive females. The aggressive behaviors between males within a group were not significantly different in the frequency of overall aggressive interactions per OHU between the two species. However, the types of aggressive behaviors observed differed between the species. Severe aggressive interactions such as aggressive physical contact among adult males were not observed in bonobos. Comparison of the results suggests the considerable influence of maternal support on the substantial differences in aggressive interactions between the two species. Among bonobo males, most aggression occurred between the sons of the two highest-ranking females.

In bonobos, females sometimes participated in polyadic aggressive behaviors as the aggressor, whereas all cases of coalitionary aggression in chimpanzees were from male aggressors. Alpha male status is strongly affected by the dominance status of the mothers and their support in bonobos. This is also likely because of the long-lasting and close mother–son relationship and the high dominance status of the females. The strong lifelong relationship between mothers and sons in bonobos is influenced by their strong gregariousness and the tendency of bonobo females to range in a central part of mixed-sex parties. This study has highlighted the differences in male aggression between bonobos and chimpanzees based on data obtained using the same method.

Chapter 4 General discussion

A comparison of the male–male relationships between bonobos and chimpanzees showed the large difference in male competition between the two species. In chimpanzees, what matters in male competition in mating success is the strength of the males themselves and their cooperation with other males. On the contrary, these factors seem to have little effect on the mating competition among male bonobos when there is strong maternal support. In chimpanzees, males need to manage the risk of intense aggression, as observed in Chapter 2, although most males can have opportunities to succeed in mating competitions. There is a low risk of aggression in bonobo males, although only a handful of males can succeed in the mating competition. Results of Chapter 3 suggested that this difference in male behaviors between the two species might be strongly affected by the difference in maternal support. In bonobos, alpha male status is strongly affected by the dominance status of the mothers and their support. This is likely because of the long-lasting and close mother–son relationship and the high

dominance status of the females. The strong lifelong relationship between mothers and sons in bonobos is influenced by their strong gregariousness and the tendency of bonobo females to range in a central part of mixed-sex parties. These characteristics of society are also related to various factors, including the high social status of females, coalitions among females against males, and prolonged receptivity of females. The evolution of these female behaviors and physiology should be revealed to understand the differences in socio-sexual characteristics between chimpanzees and bonobos, and the variation and flexibility in male–male relationships of male-philopatric societies.