

Abstract of thesis

Do kinship with the silverback matter? Group formation, social relationship, and behavior acquisition in wild western lowland gorillas (*Gorilla gorilla gorilla*)

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INTRODUCTION

The genus *Gorilla* is a fascinating model to understand the evolutionary origin of dedicated human fathers because of their phylogenetical proximity and social similarities. Gorilla adult males (i.e., silverbacks) show high affiliation towards the offspring of the own group and may socially influence offspring's behavior acquisitions. Silverback-immature affiliations are considered to be based on the high paternity certainties owing to the one-male polygynous system among the species. Nevertheless, in the western lowland gorilla subspecies (*G. gorilla gorilla*), there is an increasing evidence that resident silverbacks co-reside with unrelated immatures. However, such group formation process, consequent group kin structure, and subsequent silverback-immature social relationships have not yet been completely described.

In Moukalaba-Doudou National Park, Gabon, drastic social change was caused by disintegrations of two one-male groups due to losses of the resident silverbacks between 2016 and 2018. This thesis aimed to describe the process of the social change and the consequent group reorganization observed in another one-male group. I genetically determined the kin structure of the reorganized group. Furthermore, I investigated the within-group social relationships, especially silverback-immature relationships, by using behavioral observations. I also examined whether father silverbacks socially influenced the offspring's hand preference expression using the newly discovered behavioral measure—African ginger feeding. Finally, I discussed similarities and differences between human males and western lowland gorilla males.

METHODS

The field survey was conducted in four separate periods between 2017 and 2019 in Moukalaba. From August–November 2017 and February–April 2018, I mainly observed the gorilla groups that lost the resident silverback; the migrations of the remaining

members (adult females and immature offspring) were examined by observational monitoring. From September 2018–February 2019 and July–December 2019, DNA samples were collected and behavioral studies were conducted on the reorganized one-male group. DNA was extracted from the fecal samples for parentage analysis using 16 microsatellite markers. During group follows, <2 m and <5 m proximity between individuals was used as an indicator of social closeness. Charging behavior of the silverback toward human observers was noted ad libitum, assuming it was his protection of other individuals who were in close proximity to the observers. Throughout all the study periods, hand use during feeding on African gingers was recorded to determine the direction of hand preference for 21 gorillas. During feeding times <2 m proximity was seen as an opportunity for social learning.

RESULTS

As a result of social change, three adult females and 12 immatures, from the disintegrated groups, immigrated into a neighboring one-male group, named Group Nidai. Group Nidai originally consisted of one silverback, two adult females, and two infants; thus, its group size increased from 5 to 20. Genetic analysis revealed that only two natal infants were genetic offspring of the resident silverback, whereas all immigrant immatures were sired by the disappeared silverbacks of their natal groups.

The related immatures spent more time within 2 m of the silverback than the unrelated immatures. Many unrelated immatures preferred the company of an adult female, who was their paternal sister in the previous natal group, more than the silverback. However, the silverback was never hostile to the unrelated immatures, but rather tolerated their close proximities, mainly when the immatures played with each other. The silverback performed charging behaviors for protecting unrelated immatures multiple times. Throughout my observations, direct affiliative interactions between the silverback and immatures were not observed regardless of the kinship.

All 21 subject gorillas showed strong hand preference at individual levels in bimanual coordinated tasks during African ginger feedings. Further, a significant group-level right-hand preference (15 right-handed and 6 left-handed) was observed. Hand preference did not run in both matrilineal and patrilineal families. All the five infants were more frequently within 2 m range of their mothers, during feeding times, and the amount of time spent within 2 m of the silverback was much less than the mother.

DISCUSSION

I have provided robust evidence that western lowland gorillas form stable and cohesive

one-male groups in which the silverback co-resides with unrelated immatures. The social closeness between the silverback and immatures varied depending on the kinship. In the case of Group Nidai, the paternal adult sister, rather than the silverback, might play a pivotal role in the immigration and assimilation of unrelated immatures into the non-natal group. However, the day-to-day close proximities between the silverback and unrelated immatures and his charging behaviors toward humans for protecting the unrelated immatures suggested that western lowland gorilla silverbacks have social tolerances toward immatures beyond kinship.

Since silverback-immature close proximities rarely occurred during feeding time, gorilla fathers are unlikely to socially influence the acquisitions of offspring's feeding behaviors, including hand preferences. However, there was no significant concordance even within matrilineal families despite several opportunities for social learning from the mother. The present study has provided informative results that attempted to validate genetic heritability and social learning using both genetic and behavioral data; my findings suggest the complex mechanism underlying hand preference expression.

This study suggests that a phenomenon similar to the stepfather-stepchildren affiliation in human societies is also observed in western lowland gorillas. On the other hand, western lowland gorilla silverbacks do not seem to develop human-like enthusiastic direct cares. Additionally, father silverbacks are unlikely to be an important social model in offspring's behavior acquisition, unlike human fathers.