学位論文の要約

題目: Proximate causes of natal transfer in female bonobos

(ボノボのメスにおける出自集団からの移籍に関する至近的要因)

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General Introduction

Dispersal from the natal group to an unfamiliar group (i.e., natal transfer) is an important milestone of an individual's life history. The dispersal strategy favored by selection can be variable between and even within species. Unlike a popular pattern of female philopatry among mammals, the two Pan species, bonobos (P. paniscus) and chimpanzees (P. troglodytes), exhibit a similar pattern in that females typically transfer between groups as a nulliparous state and males have a strong residency in their natal group throughout their lives. They also share basic socio-ecological and physical characteristics, e.g., feeding primarily on ripe fruits, grouping with fission-fusion dynamics, and swelling the perineum skins. However, long-term data of demography in wild populations have revealed that female bonobos transfer out of the natal group at a younger age than female chimpanzees. The timing of female transfer can be associated with social structures of the species. For example, female bonobos form a wide range of affiliative relationships with unrelated females, while female chimpanzees make a longlasting social bond with a few specific partners. In addition, female bonobos achieve equal or higher social status as the male conspecifics, in contrast to the female chimpanzees which remain subordinate to all adult males. Nonetheless, while inbreeding avoidance provides a plausible explanation for female transfer in primates generally, physiological, behavioral, and social changes behind natal transfer in female bonobos and chimpanzees specifically are poorly understood.

Particularly, there have been less studies on young female bonobos in the wild. The aim of

my research was to document behavioral and hormonal changes in young female bonobos so as to potential proximate mechanisms for the timing of their natal transfer. Chapter 2 described the investigation of age-related changes in party associations with mothers in juvenile bonobos. Chapter 3 investigated pubertal changes in sexual hormone and copulative behaviors prior/posterior to natal transfer. Chapter 4 analyzed a pattern in agonistic interactions from resident females toward recent immigrant females. Behavioral observations and non-invasive urine samples were all collected in habituated groups of wild bonobos at Wamba, in the Luo Scientific Reserve, the Democratic Republic of the Congo. In the study groups, there has been no case in that female bonobos remain in their natal groups until they give birth to first infants.

Chapter 2

Mothers are the most fundamental individuals for the survival and development of infant and even juvenile primates. Differences in social relationships with mothers between offspring sexes during the juvenile period and across species can be one of the key aspects of understanding specific patterns of social integration into adult social lives. I calculated dyadic association indices of mother-offspring pairs (DAI-MOs), using long-term member sets collected with a "one-hour party" method. I compared DAI-MOs between offspring sex within each age class with a Generalized Linear Mixed Model (GLMM). I found that female bonobos less associated with their mothers than male bonobos between 6 and 7 years old. The dissociation from mothers is likely to precede the timing of natal emigration (6.78 ± 0.25 years old). My result implicates that female bonobos begin the dissociation from mothers at an earlier age than female chimpanzees that emigrate at 11-13 years old. High tolerance of female bonobos toward unrelated females may enable spatial independence of daughter from their mothers at an earlier stage compared to chimpanzee daughters in the similar age.

Chapter 3

Natal transfer is often correlated with hormonal and behavioral changes during puberty. However, some previous studies have mentioned that female bonobos can emigrate before exhibiting sexual skins and developing sexual interactions. I examined whether their ovulation precedes the timing of natal emigration by measuring urinary estrone conjugates (E₁C) and pregnanediol-3-glucuronide (PdG) levels (major urinary metabolites of estrogens and progesterone known to reflect ovarian function in the bonobos). Urine samples were collected with filter papers and analyzed with enzyme immunoassays. As a result, any ovulatory signals implied by a sustained rise of PdG levels were not detected until at least one year after emigration. On the other hand, I found that E₁C levels and copulation rates increased from before the emigration and continued rising thereafter until they reached a peak. My results suggest that female bonobos may emigrate at an early stage of puberty when gonadotropins begin to stimulate estrogen production but follicular development fails to reach ovulation. I propose that the prolonged time between natal emigration and sexual maturation might benefit them for their future reproductive careers.

Chapter 4

Resistance of resident females to immigration is an expected manifestation of feeding competition and prevents immigrant females from smoothly taking advantage of group life. In bonobos, however, immigrant females are likely to integrate smoothly into an unfamiliar group through affiliative interactions with specific senior females. Old resident females might gain an indirect benefit from female immigration by increased mating opportunities for their philopatric sons. I examined the effect of (1) age and tenure and (2) the presence of mature sons on the probability of aggression by resident females against immigrant females, which were defined

with a group tenure of less than 2.5 years. Immigrant females were positioned in the bottom of female dominance hierarchy that correlated with age and tenure. I found that the rate of aggression against immigrant females decreased with age in resident females but was unrelated to the presence of mature sons. My results imply that older females indeed are comparatively tolerant to immigrant females irrespective of their reproductive advantage they accrue if their sons breed with the new females.

Conclusion

My research highlights that the earlier transfer of female bonobos compared to female chimpanzees may be realized by high female gregariousness regardless of kinship and familiarity. One conceivable benefit of the prolonged period between natal transfer and sexual maturation is to postponing the energetic costs of gestation and lactation until immigrant females become familiar with the established group. Another strategy is allocating more time to seek better groups based on food availability and male quality. More extensive and longitudinal sampling on a large number of female bonobos is needed to better understand their specific strategy for natal transfer.