Proximate causes of natal transfer in female bonobos

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2020

Primate Research Institute

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Abstract

My research aimed to examine the proximate causes of natal transfer in female bonobos (*Pan paniscus*) and discussed socio-ecological factors behind its pubertal event in comparisons with female chimpanzees (*Pan troglodytes*). Although females of the *Pan* species typically transfer from the natal group to another group only before the first reproduction, female bonobos disperse at a younger age than female chimpanzees. The timings of female transfer might be related to differences in social characteristics of the species. In this study, I focused on social relationships and maturational statuses of female bonobos before/after their natal transfer. Behavioral observations and non-invasive hormone assays were conducted on habituated groups of wild bonobos at Wamba, in the Luo Scientific Reserve, Democratic Republic of the Congo. In Chapter 2, I presented that female bonobos began dissociation from their mothers at an earlier age than male bonobos and that this sex difference is in contrast to that of female chimpanzees. In Chapter 3, I demonstrated that the increase in urinary estrone conjugates (E_1C) and copulation rates preceded the time of female transfer, and ovulatory signals implied by a sustained rise of urinary pregnanediol-3-glucuronide (PdG) were detected one or two years after transfer. In Chapter 4, I showed that new immigrant females were positioned at the lowest ranks in the female dominance hierarchy and less often aggressed by older resident females than younger resident females, irrespective of having mature sons. My research revealed that female bonobos transfer out of the natal group after the weakened relationships with their mothers, at the early stage of puberty. When compared with chimpanzees, I suggest that high female tolerance regardless of kinship in bonobos might reduce the fitness costs associated with natal transfer and facilitate the early dispersal of female bonobos relative to sexual maturation. The early dispersal of female bonobos might play an adaptive function in their future reproductive careers.

Acknowledgements

This study was conducted under the supervision of Dr. Furuichi, T. I am grateful to his consistent support and advice, and for giving me opportunity to conduct my fieldwork at Wamba, in Luo Scientific Reserve, Democratic Republic of the Congo (DRC).

I really appreciate Dr. Idani, G., Dr. Simizu, K., Dr. Hashimoto, C., and Dr. Hayashi, M. for their helpful suggestions and comments on my manuscript. I am very grateful to all members of Social Ecology Section in Primate Research Institute, especially Dr. Yumoto, T., Dr. Hashimoto, C., Dr. Takemoto, H., Dr. Sakamaki, T., Dr. Hohman, M., Dr. Hanya, G., Dr. Tsuji, Y., Dr. MacIntosh, A., Dr. Ryu, H., Dr. Tokuyama, N., Dr. Sarabian, C., Dr. Toyoda, A., Dr. Ishizuka, S., Ms. Aruga, N., Mr. Honda, T., Mr. Okamura, H., Mr. Yokoyama, T., and Mr. Shibata, S. for their kind advice and earnest discussions, and Mouri, K. for lectures of hormonal analysis. I am also thankful to members of the Leading Program of Primatology and Wildlife Science (PWS) of Kyoto University, especially, Dr. Matsuzawa, T., the organizer of the PWS, and Dr. Idani, G. and Dr. Okayasu, N., my mentors of the PWS Leading Program.

I would like to express deep gratitude toward all local assistants of the Wamba Committee for Bonobo Research for their help of my study in the village and toward government staffs of the Center of Research for Ecology and Forestry of the DRC for various their supports in Luo Scientific Reserve. I also thank Wamba villagers for allowing and supporting my work.

This study was financially supported by the Leading Program of Primatology and Wildlife Science of Kyoto University, Grant-in-Aid for Scientific Research by the Japanese Society for Promotion of Science (17J01336), and a Young Explores Grant of National Geographic Foundation for Science and Exploration (Asia 38-16).

Finally, I would like to express great thanks for my family, parents, grandparents, and brothers, who support my works.

Chapter 1: General Introduction

1. Biological dispersal

Dispersal, the movement of an individual between habitat patches or social units, is a key component of an individual's life history by influencing the spatial, genetic, social, and demographic structure of a population (Clobert et al. 2009; Guerrini et al., 2014; Ronce 2007). The dispersal strategy favored by selection can be variable between and even within species (Shaw and Kokko 2014). The evolutionary mechanisms underlying variation in dispersal have been a fundamental research question in biology (Bowler and Benton 2005; Clobert et al. 2001; Greenwood 1980; Trochet et al. 2016). Theoretical studies have proposed several potential factors driving dispersal, e.g., inbreeding avoidance, kin competition, resource competition, and environment stochasticity (Henry et al. 2016; Johnson and Gaines 1990; Koenig 2002; Lambin et al. 2001; Moore and Ali 1984; Pusey and Wolf 1987; Trivers 1974). However, empirical studies on the causes and consequences of dispersal in many species remain insufficient (Clobert et al. 2012). Measuring and modeling dispersal in time and space have been a challenging issue because the interaction between an individual's history and the social and environmental context is all associated with why, when, and where the individual disperses (Bonte et al. 2012; Koenig et al. 1996; Trochet et al. 2016).

2. General dispersal patterns in mammals

In contrast to resident conspecifics, dispersers generally often face a larger fitness cost (Bonte et al. 2012; Isbell and van Vuren 1996) such as predation risk (Holzenbein and Marchinton, 1992; Isbell 1990), energetic loss (Maag et al. 2019; Rosen and Trites 2002), and social stress (Crockett and Pope 1988; Soulsbury et al. 2008). For group-living animals, dispersal from a familiar social unit to another social unit is referred to as “transfer (social dispersal)” that is comprised of “emigration,” “intergroup movement,” and “immigration” (Isbell and van Vuren 1996). For territorial species, transfer coincides with “locational dispersal” from a familiar habitat to another habitat (Isbell and van Vuren 1996). The transfer cost from the natal group (natal transfer) is expected to be larger when young individuals leave their natal habitat and dissociate from familiar conspecifics, including their mothers. For example, aggression from resident conspecifics toward foreigners is a major documented cost of dispersal, as unfamiliar individuals often evoke more aggression than familiar conspecifics (Albert et al. 1989; Boydston et al. 2001; French and Inglett 1989). When an individual attempts immigration into an established group, aggression from resident conspecifics may prevent it from smoothly taking advantage of group life such as increased protection against predation, local knowledge of home ranges, and cooperative defense of food resources (Alexander 1974; McComb et al. 2001; van Schaik 1983). The pattern and timing of transfer for each sex and species may be affected by the potential cost during each of the transfer phases (Alberts and Altemann 1995; Bonte et al. 2012; Perrin and Mazalow 2000).

Among mammals, females are generally philopatric or disperse a shorter distance from their natal area than do males (Clutton-Brock and Lukas 2012; Greenwood, 1980; Handley and Perrin 2007; Pusey and Packer 1987; Trochet et al. 2016; Wild and Taylor 2004). Factors limiting female dispersal include energetic requirements for gestation, parturition, and infant care. On the other hand, males, with a comparatively smaller investment in offspring, may disperse a long distance to search for better food resources or look for mates. Further, philopatry can be advantageous to females because accumulated knowledge of their natal areas enhances the feeding efficiency and safety (Ali 1981; Brent et al. 2015; McComb et al. 2001) on which female reproductive success depends (Trivers 1972; Stockley and Bro-Jørgensen 2011). This can also promote kin-related cooperative relationships among females (Clutton-Brock et al. 2012; Silk 2009). Thus, a female-biased dispersal pattern is rare relative to a male-biased dispersal pattern and occurs only sporadically among group-living mammals (Greenwood 1980; Pusey and Packer 1987; Handley and Perrin 2012). Nonetheless, female transfer, with and without male philopatry, is seen in many primate species, including African great apes, spider monkeys, woolly spider monkeys, muriquis, and red colobus monkeys (Moore 1984; Lee and Strier 2015). The strategies of female transfer in environmental and social contexts are an important topic in primatology (Jack and Fedigan 2009; Printes and Strier 1999; Robbins et al. 2009; Sterck et al. 1997; Stumpf et al. 2009).

3. Why female bonobos transfer at a younger age than female chimpanzees?

The two *Pan* species, bonobos (*Pan panisucus*) and chimpanzees (*Pan troglodytes*), have diverged an estimated 1.0–1.8 million years ago (Caswell et al. 2008; Takemoto et al. 2015; Yu et al. 2003). They share basic socio-ecological characteristics; both species feed primarily on ripe fruits and form multi-male/multi-female groups with fission-fusion grouping dynamics (Boesch and Boesch-Ackermann 2000; Goodall 1968; Hashimoto et al. 2003; Kano, 1982; Nishida 1968; Lehmann and Boesch 2004; Lehmann et al. 2007; White 1988). They also exhibit a similar pattern in that females usually transfer between groups as nulliparous adolescents and males have a strong residency in their natal group throughout their lives (Goodall 1986; Nishida et al. 2003; Kano 1992; Hashimoto et al. 2008). Unlike several other species with female dispersal (e.g., Crockett 1984; Monard et al. 1996; Mutschler et al. 2000), it has not been reported in the *Pan* species that other group members evict pubertal females from the natal group. Females of the *Pan* species appear to voluntarily transfer out of the natal group for outbreeding rather than to avoid kin and resource competition (Clutton-Brock 1989; Walker and

Pusey 2020; Isbell 2004).

Long-term field observations have revealed an age difference in female transfer between the *Pan* species (Table 1-1): female bonobos emigrate at six to eight years old (Lee et al. 2019; Sakamaki et al. 2015) while female chimpanzees emigrate at eleven to thirteen years old (Witting and Boesch 2019; Nakamura 2015; Stumpf et al. 2009; Walker et al. 2018). Female chimpanzees are described as exhibiting swelling of the perineum skin prior to natal emigration (Fig. 1-1), and they copulate with mature males in the natal group when they become estrous (Nishida, 1979; Pusey, 1990; Stumpf et al., 2009). By contrast, female bonobos still appear to be immature in their genital areas (Fig. 1-2) and have copulatory interactions with mature males less often before leaving the natal group (Hashimoto, 1997; Sakamaki et al., 2015). The developmental thresholds at natal transfer are likely to be different between these close species, which may be determined by the socio-ecological factors of each.

This age difference might be explained by the different costs of female transfer between the *Pan* species. In chimpanzees, immigrant females may suffer intense aggression from resident females due to competition over food resources (Boesch and Boesch-Ackermann 2000; Kahlenberg et al. 2008b; Pusey et al. 2008). In contrast, female harassment toward immigrant females has not been reported in bonobos (Idani 1991; Sakamaki et al., 2015). Additionally, opportunities to assess a neighboring group before natal emigration are likely to be abundant in bonobos due to frequent and affinitive intergroup encounters (Idani 1990; Sakamaki et al. 2018; Tokuyama et al. 2019) while such an opportunity seems to be relatively limited because of hostile intergroup relationships in chimpanzees (Boesch et al. 2008; Williams et al. 2004). Thus, energetic loss and social stress in the process of female transfer in bonobos are expected to be smaller due to high social tolerance than those in chimpanzees, thereby female bonobos might transfer out of their natal group at a younger stage which is vulnerable to predators and conspecifics.

4. Thesis aim and outline

Few studies have examined the physiological, behavioral, and social changes behind female transfer in wild bonobos. The aim of my research was to investigate the proximate causes of natal transfer in female bonobos to reveal how they achieve natal transfer at a younger age compared to female chimpanzees. Data were collected in habituated and identified bonobo groups at Wamba, in the Luo Scientific Reserve, Democratic Republic of the Congo. Identifying the developmental stage at emigration from the natal group in female bonobos and investigating the social environment of the established group they immigrate may give us clues to a better understanding of their dispersal strategy.

Mothers are the most fundamental social partners for the survivorship and development of immature offspring (Nowell et al. 2007; Nicolson 1987; Watts and Pusey 1993). Differences in social relationships with mothers between offspring sexes during the juvenile period and across species may be one of the key aspects of understanding specific patterns of social integration into adult social lives (Cords et al. 2010; Kulik et al. 2016; Tolentino et al. 2008). In Chapter 2, I will describe the investigation of how female and male bonobos change associations with their mothers depending on age. Bonobos live in fission-fusion grouping dynamics where members of sub-groups (i.e., parties) change depending on socio-ecological contexts (Hohmann and Fruth 2002; Kuroda 1979; Mulavwa et al. 2008; White 1988). Mother-offspring associations were calculated as “dyadic association indices” (Cairns and Schwager 1987) using long-term datasets collected with a “one-hour party” method (Hashimoto et al. 2001). I examined the sex difference in age-related changes in associations with mothers.

Natal dispersal to avoid inbreeding can be an important pubertal event in an individual’s life history (Clutton-Brock, 1989; Pusey and Wolf 1996). Female bonobos emigrate from the natal group at a young stage, before sexual swelling and copulative behaviors occur (Hashimoto 1997; Sakamaki et al. 2015). Chapter 3 describes the investigation of hormonal and behavioral changes during puberty in nulliparous female bonobos before/after natal emigration. I assayed urinary concentrations of estrone conjugates (E_1C) and pregnanediol-3-glucuronide (PdG) corrected with creatinine volumes, using enzyme immunoassays (Shimizu and Mouri et al. 2018). I also observed their copulatory interactions with adolescent and adult males. I checked whether ovulation defined by a sustained rise of PdG levels (Douglas et al. 2016; Ryu 2017), occurred before the emigration and examined whether the increase in E_1C levels and copulation rates preceded the date of emigration. Through this process, I identified the pubertal stage in female bonobos at natal emigration.

Aggression from resident females toward immigrant females is an expected manifestation of the increased costs of intrasexual competition outweighing the benefits of group life in species with female transfer (Crockett 1984; Watts 1991). Referring to the previous finding that immigrant female bonobos can be smoothly integrated through affiliative interactions with old resident females (Idani 1991), I hypothesized that older female bonobos are tolerant toward immigrant females to benefit from the increase in mating opportunities for their philopatric sons. Chapter 4 details the investigation of aggression patterns in resident females toward immigrant females defined with a group tenure of less than 2.5 years, the mean interval between immigration and first parturition (Sakamaki et al. 2015). I first calculated David’s scores from the matrix of agonistic interactions (David 1987) and examined the steepness and linearity of the female dominance hierarchy (de Vries et al. 2006). I then examined the effect of age and the presence of mature sons on the probability of aggression toward immigrant females.

My research highlights the difference in dispersal strategies between the *Pan* species based on socio-ecological conditions. In Chapter 5, I summarize the results of my research and discuss the proximate causes of natal transfer in female bonobos. I suggest that the lower threshold for female transfer in bonobos may result from the higher social tolerance of female bonobos compared to female chimpanzees. I then propose two conceivable benefits behind the early timing of natal emigration relative to sexual maturation. Finally, I mention the limitations of my research and future perspectives for a better understanding of the transfer strategies in female bonobos.

Table 1-1. Age of natal emigration in female bonobos and chimpanzees.

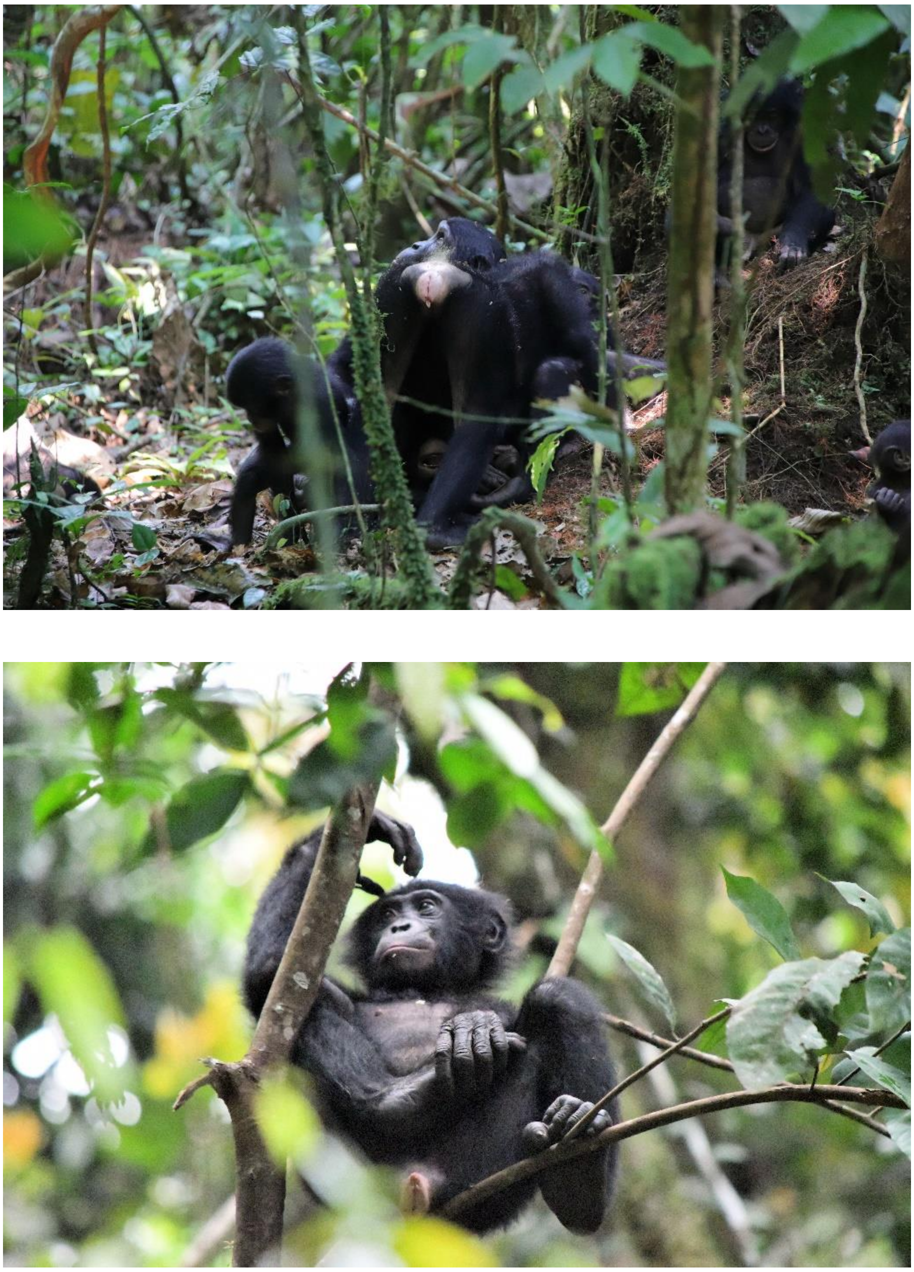
Species	Site	Age at emigration
Bonobo	Wamba[1]	est. 6–9 y (14)
(*Pan paniscus*)	Lui Kotale[2]	ca. 6.5–7.5 y (2)
	Gombe[3]	12.23 ± 0.54 y (12)
Chimpanzee	Kanyawara[4]	12.60 ± 1.00 y (9)
(*Pan troglodytes*)	Mahale[5]	11.38 ± 1.42 y (24)
	Tai[6]	11.85 ± 0.78 y (9)

[1] Sakamaki et al. 2015; [2] Lee et al. 2019; [3] Walker et al. 2018; [4] Stumpf et al., 2009; [5] Nakamura 2015; [6] Wittig and Boesch 2019. Sample size is indicated in parentheses.

Fig. 1-1. Perineum skin swelling of female chimpanzees at a suitable age for natal emigration

This picture provided by Matsumoto T. at Mahale is of a twelve-year-old female chimpanzee.

Fig. 1-2. Perineum skins of female bonobos at a suitable age of natal emigration



The upper picture, taken by Tokuyama N. at Wamba, is of Mazy at six years old in 2019. The lower picture, taken at Wamba is of Jolie at seven years old in 2019.

Chapter 2

Age and sex differences in associations with mothers in juvenile bonobos at Wamba

1. Abstract

Mothers are the most fundamental individuals for the survival and development of immature offspring. Sex-biased dispersal may have a consequence on strong and long-lasting social bonds between mothers and their philopatric offspring. This assumption has been supported in several primate species with male-biased dispersal species. However, it has not been applied to primate species with female-biased dispersal. Bonobos (*Pan paniscus*) are unique among female-biased dispersal species in that females exert influence on male reproductive competitions for their matured sons and tolerate with each other irrespective of kinship. Fewer studies have examined the mother-offspring relationship as it pertains to cooperative patterns in adult bonobos. I investigated how juvenile male and female bonobos undergo a change in association with their mothers depending on age at Wamba, Democratic Republic of Congo. I observed a behavioral difference between sexes; for example, female bonobos reduced associations with their mothers prior to the timing of emigration from the natal group. In contrast, male bonobos maintained relatively high associations with their mothers through their juvenile years. My results in bonobos appear to be different from the previous findings in chimpanzees (*Pan troglodytes*) where males begin to reduce associations with their mothers earlier than females and strengthen their associations with adult males in the natal group. I suggest that high social status of female bonobos may extend maternal support for philopatric sons. Further, their high tolerance to unrelated females may allow female bonobos to dissociate from their mothers at an earlier stage compared to female chimpanzees in the similar age.

2. Introduction

Primates spend a more extended period of juvenility between weaning and maturity than other mammals with similar body sizes (Kappeler et al. 2003; Pagel and Harvey 1993). Mothers are necessary for the nutrition and locomotion of infant primates (Nowell et al. 2007; Nicolson 1987), where even after weaning, mothers can continue to be the most basic social partner for juvenile primates (Watts and Pusey 1993). The juvenile period is a critical time for primates to reduce association with their mothers and begin forming social relationships with others for successful social integration into adulthood (Pereira and Fairbanks 1993). Juvenile social relationships are hypothesized to be affected by adult cooperative relationships (Cords et al. 2010; Fairbank 1993; Nicolei and Borries 1997). The difference in social relationships with mothers determined by offspring sex and species may be the primary characteristic in understanding specific patterns of social integration depending on socio-ecological factors.

Sex-biased dispersal pattern is assumed to an important factor to drive strong and long-lasting social bonds between mothers and philopatric offspring (Clutton-Brock and Lukas 2012; Silk 2009). Sex-biased dispersal is defined as when one sex typically leaves the natal group while the other sex remains (Trochet et al. 2016). Since natal dispersal is a decisive event that will result in the unavailability of mothers, dispersing offspring tend to intensify dissociation from their mothers before leaving the natal group (Colvin 1986). In contrast, philopatric offspring have the option of utilizing their mothers; e.g., taking advantage of dominance rank acquisition (Chapais et al. 1997; de Waal 1993; Walter 1980). Previous studies on primate species with a male-biased dispersal pattern demonstrated that juvenile females maintained a closer social bond with their mothers compared to juvenile males (e.g., Japanese macaques, *Macaca fuscata*, Nakamichi 1989; rhesus monkeys, *Macaca mulatta*, Kulik et al. 2016; blue monkeys, *Cercopithecus mitis*, Cords et al. 2010).

However, the assumption is not necessarily applicable to all primate species, particularly in female-biased dispersal species. A female-biased dispersal pattern is common in *Pan* and *Atelinae* primates (Lee and Strier 2015), which are characterized by a multi-male/multi-female social unit with a degree of fission-fusion grouping dynamics (Strier et al. 2014). In addition, these females tend to remain in the reproductive group (Nakamura 2015; Sakamaki et al. 2015; Strier et al. 2015; Wittig and Boesch 2019; Link et al. 2018), and thus they live with their philopatric sons in the same group for a long period. Previous studies have documented that male offspring reduce associations with their mothers earlier than female offspring or at similar ages (e.g., chimpanzees, *Pan troglodytes*: Hayaki 1988; Pusey 1983; Geoffroy's spider monkeys, *Ateles geoffroyi*: Rodrigues 2007; northern muriquis, *Brachyteles hypoxanthus*: Tolentino et al. 2008). For example, juvenile male chimpanzees begin to increase associations and social interactions with mature males in their natal group, which can be required to cooperative territorial defense against males from adjacent groups (Aureli et al. 2006; Gilby and Wrangham 2008). On the other hand, juvenile female chimpanzees maintain high associations with their mothers exclusively until sexual maturity. Furthermore, even after sexual maturity, several female chimpanzees will stay in the same core area with their mothers (i.e., small areas of intense use within the home range), in which the quality of food resources is related to female reproductive success (Kahlenberg et al. 2008b; Thompson et al. 2007; Walker et al. 2018).

Bonobos (*Pan paniscus*) are a unique species among primates with a female-biased dispersal pattern in that male offspring maintain lifelong associations with their mothers among primates with male philopatry (Furuichi 1989; Surbeck et al. 2017). Additionally, the presence of bonobo mothers affects the reproductive success of their sons. However, this influence is not observed in chimpanzees (Surbeck et al. 2019). Female bonobos are codominant with males (Furuichi 1997; Parish 1994) and tend to occupy higher ranks than males within the group

(Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016), in contrast to female chimpanzees which remain subordinate to all adult males (Muller et al. 2009; Stumpf and Boesch 2010). This codominant social structure may enable bonobo mothers to directly influence mating opportunity of their sons (Furuichi 1997; 2011; Surbeck et al. 2011; 2019). Furthermore, affiliative and cooperative relationships among unrelated females are one of the primary characteristics in bonobos (Moscovice et al. 2017; Tokuyama and Furuichi 2016). For example, female tolerance is not only limited to within-group females but also extends to out-group females (Idani 1990; Tokuyama et al. 2019), where they can be comparatively tolerant toward immigrant females (Idani 1991), as opposed to female chimpanzees who seem to be hostile toward immigrant females (Boesch and Boesch-Ackermann 2000; Kahlenberg et al. 2008b; Pusey et al. 2008). However, little is known regarding the social construct between juvenile bonobos and their mothers in corresponding to unique social behaviors in adult bonobos.

The aim of this study was to investigate how female and male bonobos change associations with their mothers during the juvenile period. Based on the hypothesis that juvenile social relationships are shaped by adult cooperative relationships (Cords et al. 2010; Fairbank 1993; Nicolei and Borries 1997), given cooperative patterns in adult bonobos, I predicted juvenile female bonobos to decrease associations with their mothers, and juvenile male bonobos to maintain associations with their mothers throughout the juvenile period. From long-term records of memberships comprising fission-fusion parties in wild bonobos at Wamba, I examined an interactive effect between offspring sex and offspring age on associations with their mothers. This study will serve to provide a deeper understanding of how the unique social roles of female bonobos, among female-biased dispersal species, affect sex-specific ontogenetic trajectories in associations with their mothers.

3. Methods

3-1. Study subjects

Observations of this study were conducted on two wild bonobo groups, called “E1” and “PE”, at Wamba, in the northern sector of the Luo Scientific Reserve, Democratic Republic of the Congo (Kano 1992; Furuichi et al. 2012). Data were collected on the E1 group during six different periods (3 to 6 months per period) and in the PE group during the second to sixth periods: November 2014–February 2015 (Period 1), July–October 2015 (Period 2), May–October 2016 (Period 3), February–July 2017 (Period 4), February–June 2018 (Period 5), and December 2018–March 2019 (Period 6). During the study periods, the E1 group consisted of 31–43 individuals (including 9–12 adult females and 7–8 adult males), while the PE group consisted of 24–28 individuals (including 9 adult females and 4–5 adult males).

I collected data on eleven female and eight male offspring during the juvenile period from ages 4 to 8 years (Hashimoto 1997), and there were no orphans in the E1 and PE groups (Table 2-1). All subjects were identified from their birth. The maximum age estimation error of offspring subjects was less than one month, as all mothers returned with their newborn offspring within a month after missing from their groups without offspring. Females that disappeared from their natal group in visibly good health upon final observation or, when females immigrated into neighboring groups, they were considered as having emigrated from the natal group. During my study periods, six juvenile females left their natal groups and never returned. One juvenile male (KL) also disappeared in visibly good health; however, I did not determine whether he dispersed or died There have been no records of male immigration to the study groups since the beginning of observation with individual identification in 1976, except for a few cases that occurred after the extinction of some neighboring groups during war in DR. Congo (Hashimo to et al. 2008).

3-2. One-hour party

Bonobos were followed daily by researchers and assistants from their night bed sites (approximately 06:00) until they made new night beds (approximately 17:00; Mulavwa et al. 2010). I followed the E1 and PE groups for 2655 hours in 339 days (7.83 ± 2.46 hours per day) and 1035 hours in 143 days (7.23 ± 2.40 hours per day), respectively. When group members split into two or more temporary parties (Kuroda 1979; White 1988), the largest party was followed when possible. I defined the party using a one-hour party method proposed by Hashimoto et al (2001), where party membership was determined by all the individuals observed within a one-hour interval. I recorded the individuals present from the beginning to the end of every hour. I did not include the one-hour party data unless I could observe bonobos for more than 30 min in a one-hour segment (Hashimoto et al. 2001; Mulavwa et al. 2008). Additionally, I excluded any data that resulted from intergroup encounters in order to avoid possible influences of intergroup interactions on mother-offspring associations. In total, there were 2447 and 755 segments of the one-hour party from the E1 and PE groups, respectively.

3-3. Dyadic association index

I randomly resampled a one-hour party segment for each day to avoid spatio-temporal relationship in the data set. In total, I collected 329 and 128 one-hour party segments from the E1 and PE groups, respectively. Using the one-hour party segments, I first calculated "dyadic association indices" of each mother and offspring pair (DAI-MO) for each study period, according to the following formula suggested by Cairns and Schwager (1987): (1)

$$\text{DAI-MO} = \Sigma MO / (\Sigma M+\Sigma O+\Sigma MO) \quad (1)$$

ΣM: the number of one-hour party segment that the mother was present without offspring

ΣO: the number of one-hour party segment that offspring was present without mother

ΣMO: the number of one-hour party segment that both mother and offspring were present

When subjects dispersed during the study period, I calculated their DAI-MOs from one-hour party data until the date of dispersal.

3-4. Statistical analysis

My primary objectives were to examine how mother-offspring associations change with offspring age and sex. I ran generalized linear mixed models (GLMMs), using the "glmer" function of the "lme4" package (Bates et al. 2015) in the R software package (version 3.6.1., R Core Team 2019). The GLMM take account of the unbalanced repeated measure (Cnaan et al., 1997), thereby allowing me to include multiple data points from the same subject. I nested the offspring identity and study period as random variables to avoid pseudo-replications. Since DAI-MOs were not suitable for a linear model approach, I applied GLMMs with a binomial error structure linked by "logit" function (Baayen 2008). The response variables were the binomial values between the number of one-hour party segments in which the juvenile offspring co-existed with their mother (ΣMO) and the number of one-hour party segments in which the mother or offspring existed alone (ΣM + ΣO). The binomial values were linked with the "cbind" function in the GLMM.

As the main predictor in a regression model (GLMM 1), I included offspring age (4.01 to 7.83 years old), offspring sex (Female vs. Male), and the age-sex interaction. Since the effect of age on the probability of association was expected to be non-linear (i.e., quadratic curve), I also incorporated age squared (age-squared term) to achieve a reliable model. The offspring age was respectively calculated from the midpoints of each study period. To reduce the multicollinearity between predictor variables in the model due to the age-squared term and the age-sex interaction term, I centered (transformed) the age by subtracting the mean age (5.57 years old) from the age of each offspring (Robinson and Schumacker, 2009). I checked variance inflation factors (VIF) (Quinn and Keough 2002), using the function of "vif" from the package "car" (Fox and

Weisberg 2018). The maximum VIF was 4.71 and thus the multicollinearity between predictor variables was not a substantial issue of the analysis (Zuur et al. 2010). I compared the full model with the null model that only consisted of the random variables (offspring identity and study period), using the function of "anova" in R (Dobson and Bernett 2008).

To examine sex differences in the associations with mothers regarding age, I ran an additional model (GLMM 2), testing sex, age class (i.e., 4–5, 5–6, 6–7, and 7–8 years old), and the interaction between sex and age class. I pooled the data of the one-hour parties for each age class to recalculate DAI-MOs. To determine the significance of fixed effects, including the interaction between sex and age class, I conducted a Type II Wald test (Langsrud 2003), using the "Anova (case-sensitive)" function in the "car" package. I then conducted post hoc comparisons of the model, using the "emmeans" in the "emmeans" package (Lenth et al. 2019), in order to examine the effect of sex within each age class on the probability of association with mothers. The statistical significance of the full model was also tested by comparing its fit with that of the null model with the "anova" function.

3-5. Supplementary analysis

At Wamba, nulliparous female bonobos usually transfer between groups through intergroup encounters (Kano 1992; Sakamaki et al. 2015). Juvenile females can sometimes visit neighboring groups for a temporary period and come back to their natal groups. If daughters engaged in a temporary visit to neighboring groups without observations, the data of dissociation between juvenile females and their mothers have been overestimated due to the process of female trnasfer. To check this possibility, I focused on one-hour parties in which juvenile bonobos were observed and calculated the proportions of whether their mothers were present at the parties, as "one-side association indices" between mother and offspring pair (OAI-MO)." In a similar manner with the previous regression model (GLMM 1), I examined the effects of age and sex, and the interaction on the probability of association with mothers by running another model (GLMM 3).

4. Results

DAIs with mothers during the juvenile period are shown in Fig 2-1. Six female bonobos emigrated from their natal group at 6.78 ± 0.25 years old, while one male bonobo disappeared at 6.6 years old. GLMM 1, testing the effects of the age-sex interaction and age squared on the probability of association with mothers, was significantly different from the null model (χ^2 = 95.29, $df = 4$, $P < 0.001$). I found significant effects of the age-sex interaction term and the age-squared term on associations with mothers (Table 2-2). The significance of the age-sex interaction indicates that age-related associations with mothers differed between offspring sex. In addition, the significance of the age squared indicates that this model fitted a quadratic regression.

GLMM 2, testing the effects of the interaction between sex and age class on the probability of association with mothers, was significantly different from the null model (χ^2 = 116.56, $df = 7$, $P < 0.001$). Analysis of variance in this model showed a statistical significance of the age-sex interaction on associations with mothers (Type II Wald test: $\chi^2 = 21.86$, $df = 3$, $P < 0.001$). The post hoc analysis revealed that female bonobos were less associated with their mothers than male bonobos during the age class of 6–8 years, and that they did not differ during the age class of 4–6 years (Fig. 2-2; Table 2-3). Parameter estimates of the GLMM are shown in Table S2-3.

In supplementary, I gained a similar result with GLMM1 from GLMM 3 (Fig. S2-3; Table S2-4). The model was also significantly different from the null model ($\chi^2 = 72.13$, $df = 4$, $P < 0.001$). This result indicates that female bonobos decreased associations with mothers among members of the natal group compared to male bonobos. Sex difference in age-related changes in associations with mothers was unlikely resulted from the temporary visits of juvenile females.

5. Discussion

The current study demonstrated that a sex difference in DAI-MOs emerged during the juvenile period in bonobos. GLMM 1 indicates that the effect of offspring age on the probability of association with mothers differs between offspring sex and changes quadratically. GLMM 2 shows that DAI-MOs differed between offspring sex at 6–8 years old. Further, GLMM 3 resembling the result from GLMM 1 highlights that juvenile males maintained relatively higher associations with their mothers than juvenile females. My results suggest that female bonobos may decrease party associations with mothers depending on age, especially prior to the timing of natal emigration. In contrast, male bonobos may maintain relatively high associations with mothers throughout the juvenile period. My findings in bonobos appear to be in opposition to previous studies in chimpanzees where male offspring begin dissociation from their mothers earlier than female offspring (Hayaki 1988; Pusey 1983; 1990). This finding supports the assumption that the philopatric sex maintains a closer social bond with their mother than the dispersing sex (Kulik et al. 2016).

DAI-MOs in male bonobos seemed to decrease until approximately 6 years old as well as female bonobos, followed by a period of no change or a slight increase until 8 years old. My results are consistent with previous findings that male bonobos have a lifelong association with their mother (Furuichi 1989; Surbeck et al. 2017). Mature male bonobos whose mothers were alive tended to have high status, and a change in dominance between high-ranking males was likely to coincide with a change in dominance between their mothers (Furuichi 1997). Concerning the male’s fecundity, high-ranking males generally hold a primary position in the group; consequently, providing more access to estrous females (Surbeck et al. 2011). Thus, mothers may be able to support their sons to achieve high status as well as obtain greater access to females, which allows them to maximize the number of the mother's descendants. This emphasizes the need for further investigation on the effects of maternal factors, e.g., age, rank, and reproductive status, on the initial rank acquisition of male bonobos.

In chimpanzees, dominant mothers invest a longer period in their sons (Boesch 1997; Nakamura et al. 2014) and provide immature sons with more social support for agonistic interactions than subordinate mothers (Markahm et al. 2015). In addition, when left alone, adult males tend to use maternal core areas irrespective of mother presence (Murray et al. 2008). Thus, the social position of chimpanzee mothers can influence the dominance rank and nutritional status of their sons through life. However, male chimpanzees are likely to gradually leave their mothers once they become adolescents (Pusey 1990; Hayaki 1988). While reducing associations with mothers, male chimpanzees become to attempt dominating adult females, and then some of them compete against higher-ranking males (Nishida 2003; Pusey 1990; Sandel et al. 2017). The difference of son-mother associations between the *Pan* species suggests that dominance intersexual relationships may be an essential factor affecting the maternal utility for philopatric sons. Nonetheless, it is worth noting that another possibility that strong and long-lasting supportive social relationships between mothers and their sons might also be the reason for egalitarian intersexual structure in bonobos.

A previous study demonstrated that female bonobos spent more time at distances greater than 5m from their mothers since after 3 years old than did female chimpanzees (Lee et al. 2019). Though I used party association data, the current study does not contradict the previous study by Lee et al. (2019). I demonstrated that DAI-MOs in female bonobos declined sharply at a short-term period preceding the time of dispersal. Moreover, this proximate change for natal dispersal is also seen in female chimpanzees (Stumpf et al. 2009). However, my results that female bonobos disperse at an earlier age, between the ages of 6–8 years (Sakamaki et al. 2015; Lee et al. 2019) than do female chimpanzees (between the ages of 11–13 years: Boesch and Boesch-Ackermann 2000; Nakamura 2015; Walker et al. 2018) are consistent with previous studies. Physical growth with age is a critical factor in predicting the progress of independence from mothers; however, by itself, it does not determine the timing of dispersal. Female tolerance in bonobos may allow immigrant females to receive some benefits of female-female associations; for example, avoiding predators, ease of using localized resources, and cooperation against male harassment (D'Amour et al. 2006; Gottfried et al. 2019; Tokuyama and Furuichi 2017). This might explain why female bonobos can disperse into non-natal groups earlier than female chimpanzees and survive at an immature stage without having to depend on their mothers.

Alternatively, female chimpanzees can opt to remain in their natal group instead of natal dispersal, which affords them some advantages through maternal support (Foerster et al. 2015; Langergraber et al. 2009). Although the proportion of philopatry versus dispersal is highly variable, from < 50% in the Kasekela group at Gombe to less than 10% in many study groups (Pusey and Schroepfer-Walker 2013), there are possible maternal effects on the rank acquisition of non-dispersing females. For example, the non-dispersing female chimpanzees with their mothers in the same group acquired a higher initial rank compared to females without their mothers, or immigrant females (Foerster et al. 2016). Dominance rank among female chimpanzees seems to be essential, given that higher-ranking females have an advantage over lower-ranking females in foraging (Murray et al. 2006; Wittig and Boesch 2003). However, in bonobos, no cases of non-dispersing females were reported at Wamba (Sakamaki et al. 2015). Even though two cases of non-dispersing females were observed at Lui-Kotale, their rank seemed not to be enhanced by affiliative relationships with their mothers (Moscovice et al. 2017). It was also suggested that dominance rank between female bonobos is unrelated to better energy intakes or energy balance (Nurmi et al. 2018). Therefore, different degrees of local resource competition and mother effect on rank acquisition in female bonobos and chimpanzees might explain the species differences in female dispersal patterns and mother-daughter association patterns during development.

The current study is the first to demonstrate a sex difference in party associations with mothers in juvenile bonobos, suggesting that this sex difference emerged differently from juvenile chimpanzees. This contrast between the *Pan* species may support the hypothesis that juvenile social relationships are affected by adult cooperative relationships (Cords et al. 2010; Fairbank 1993; Nicolei and Borries 1997). I should also note the current benefits of associations with tolerant partners in juvenile primates, which are vulnerable to predators or competitors (Janson and van Schaik 1993; Pereira 1988). More detailed investigative data are needed to put forth a more comprehensive picture of juvenile social priorities (e.g., preferred social partners, the importance of social interactions).

Table 2-1. Information of juvenile offspring in the E1 and PE groups at Wamba, DRC

ID (Abbreviation)	Sex	Group	Date of birth	Date of disappearance
Nadir (Na)	F	E1	2008/09/03-09	2015/09/05–15[a]
Natsuko (Nt)	F	E1	2009/05/10–15	2015/11/06[b]
Yume (Ym)	F	E1	2009/10/06–07	2016/08/01[b]
Otoko (Ok)	F	E1	2010/12/24–2011/01/11	2017/07/04[b]
Fua (Fa)	F	E1	2010/12/29–2011/01/06	2018/03/21[b]
Jolie (Jl)	F	E1	2012/01/13–01/21	
Mazy (Mz)	F	PE	2013/05/28–06/13	2019/06/27[b]
Puka (Pk)	F	PE	2013/03/16–18	
Sato (So)	F	PE	2013/05/28–06/13	
Kalin (Kx)	F	E1	2014/01/29–02/03	
Hana (Ha)	F	E1	2014/02/25–26	
Kyota (KY)	M	E1	2009/06/25–07/06	
Hachiro (HC)	M	E1	2009/08/23–29	
Hideo (HO)	M	PE	2011/02/05–15	
Seco (SE)	M	E1	2011/12/10–13	
Kale (KL)	M	PE	2012/03/16–27	2018/11/08[c]
Isao (IA)	M	PE	2012/03/21–/04/11	

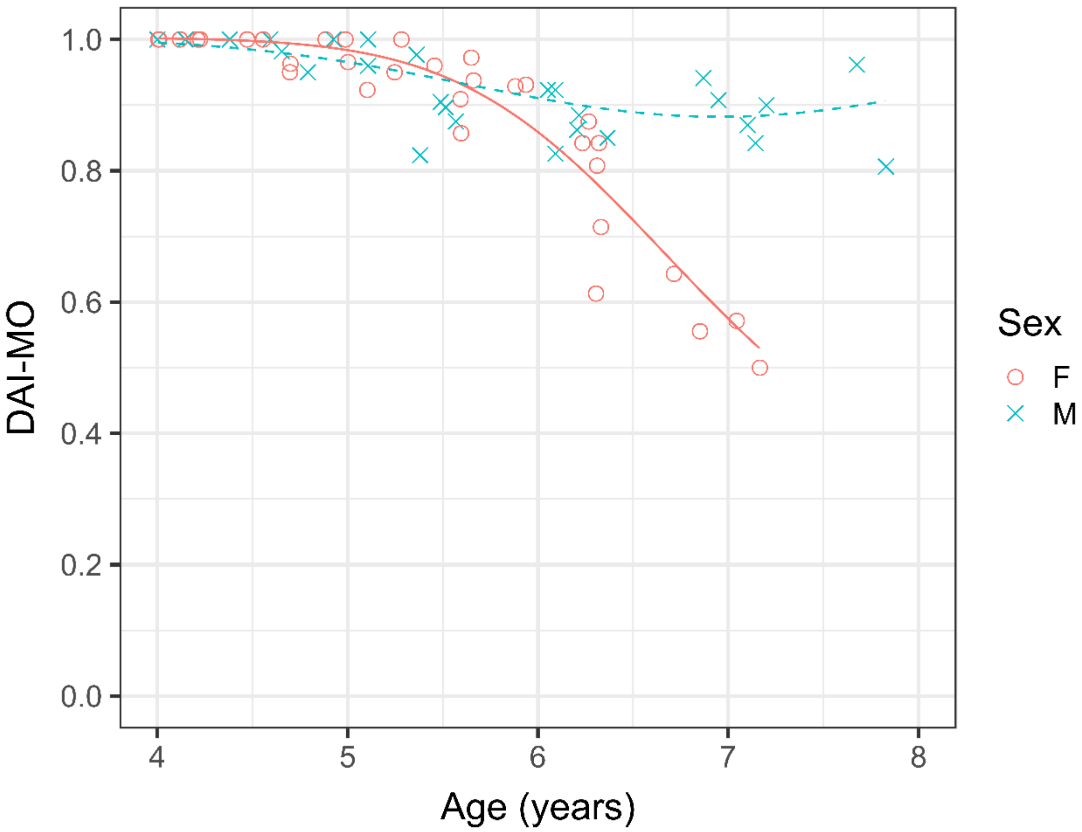
Nimba (NI)	M	E1	2013/07/06–12
Yoda (YD)	M	E1	2014/03/30–04/07

[a] Na disappeared when I lost bonobos from the E1 group at an eastern edge of their home range that overlapped with another neighboring group.

[b] They transferred into other neighboring groups through intergroup encounters.

[c] KL disappeared on the day the PE group encountered a neighboring group. I could not confirm if this individual immigrated into the neighboring group. Even though the group encounter continued the following day, I did not observe him again. This indicates his death or dispersal to the third group (though less likely).

Fig. 2-1. Age-related changes in DAI-MOs by offspring sexes



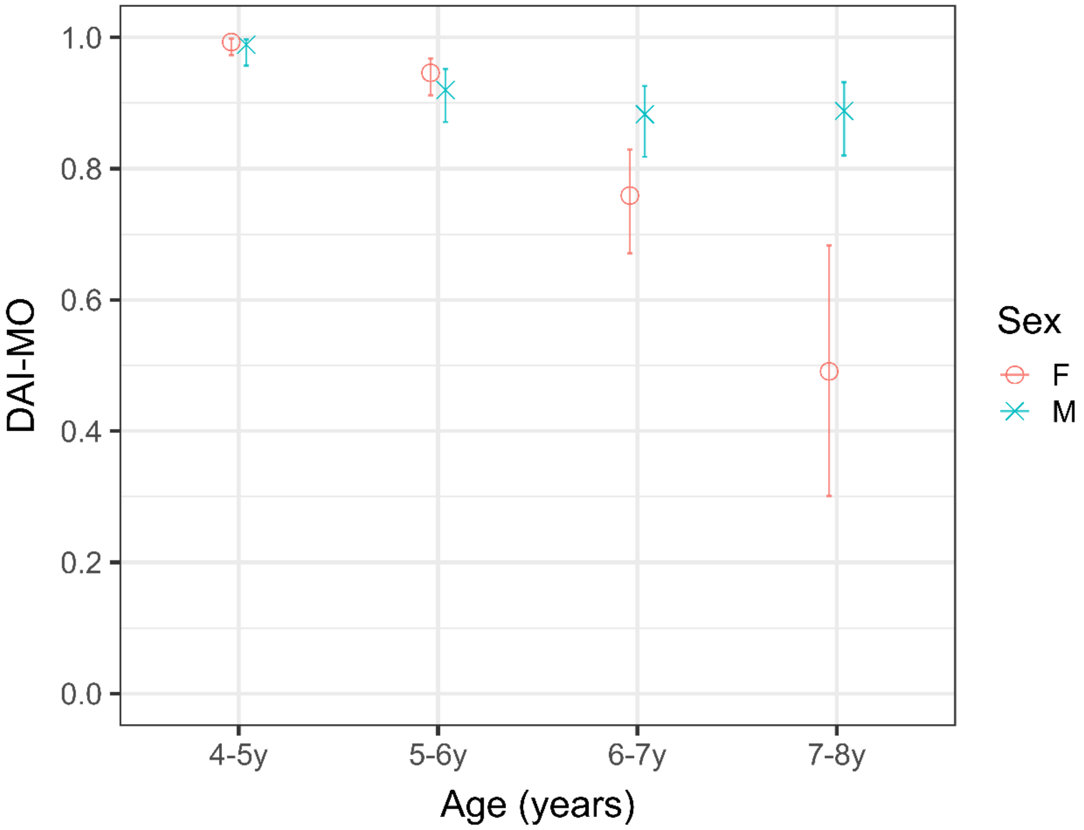
The X-axis represents the age of juvenile bonobos and the Y-axis represents the DAI-MOs. Each marker corresponds to data points from 11 female and 8 male offspring for six study periods. The two regression lines depicted from GLMM 1 indicate sex-typical changes with age in the probability of association with mother.

Table. 2-2. Parameter estimates of GLMM 1 for DAI-MO

Term	**Estimate**	***SE***	***Z***	***P***
(Intercept)	2.613	0.221	11.83	< 0.001
Age	–2.103	0.258	–8.14	< 0.001
Sex (F vs. M)	–0.115	0.301	–0.38	0.703
Age-Sex interaction	1.194	0.274	4.36	< 0.001
Age squared	0.330	0.126	2.63	0.008

Significance for the fixed effect of offspring sex and age does not have a meaningful interpretation because the age-sex interaction is significant ($P < 0.05$).

Fig. 2-2. Tukey's pairwise post hoc comparisons for associations with mothers for age classes between juvenile female and male bonobos



The X-axis represents four age class of juvenile bonobos between 4 and 8 years and the Y-axis represents the DAI-MOs. The markers and error bars represent the respective predicted value and 95% confidence intervals from output of the GLMM 2.

Table 2-3. Parameter estimates for post hoc comparisons for DAI-MO

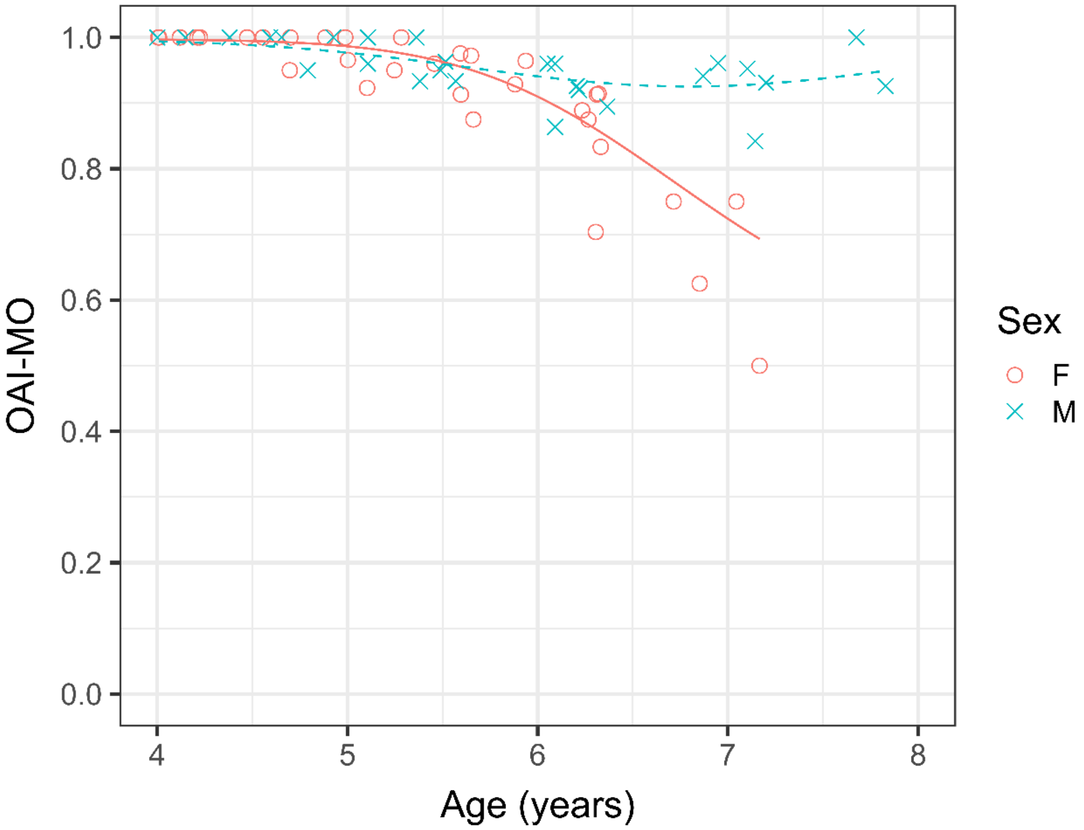
Age Class (y)	**Sample Size**		**Estimate**	***SE***	***Z***	***P***
	F	M				
4–5	8	6	0.447	1.022	0.44	0.662
5–6	9	7	0.423	0.384	1.10	0.270
6–7	7	6	–0.873	0.345	–2.53	0.011
7–8	2	4	–2.105	0.505	–4.17	< 0.001

Significant *P*-value is < 0.05. Comparison direction is female minus male.

Table. S2-4. Parameter estimates of the GLMM 2 for DAI-MO

Term	**Estimate**	***SE***	***Z***	***P***
(Intercept)	4.982	0.719	6.93	< 0.001
Sex (F vs. M)	–0.447	1.022	–0.44	0.662
Age Class 5–6	–3.837	0.752	–2.81	0.005
Age Class 6–7	–5.018	0.736	–5.22	< 0.001
Age Class 7–8	–0.447	0.814	–6.17	< 0.001
Sex:Age Class 5–6	0.023	1.064	0.02	0.983
Sex:Age Class 6–7	1.319	1.058	1.25	0.213
Sex:Age Class 7–8	2.551	1.111	2.30	0.022

Fig. S2-3. Age-related changes in OAI-MOs by offspring sexes



The X-axis represents the age of juvenile bonobos and the Y-axis represents the OAI-MO. Each marker corresponds to data points from 11 juvenile females and 8 juvenile males for six study periods. The two regression lines depicted from GLMM 2 indicate sex-typical changes with age in the probability of association with mother.

Table. S2-5. Parameter estimates of GLMM 3 for OAI-MO

Term	**Estimate**	***SE***	***Z***	***P***
(Intercept)	2.966	0.244	12.16	< 0.001
Age	–2.112	0. 0.325	–6.49	< 0.001
Sex (F vs. M)	0.192	0.352	0.55	0.585
Age-Sex interaction	1.126	0.176	2.30	0.008
Age squared	0.405	0.126	3.37	0.021

Significance for the fixed effect of offspring sex and age does not have a meaningful interpretation because the age-sex interaction is significant ($P < 0.05$).

Chapter 3

Do females disperse at the onset of puberty? Hormonal and behavioral correlates of natal transfer in female bonobos at Wamba

1. Abstract

Natal dispersal can be an important pubertal event in an individual's life history. A female-biased dispersal pattern is common in the *Pan* species, but female bonobos (*Pan paniscus*) transfer out of their natal group at a younger age than female chimpanzees do (*Pan troglodytes*). A high tolerance of female bonobos toward immigrant females might lower the developmental threshold for social integration into an unfamiliar group. However, the physiological and behavioral changes of puberty underlying the early emigration of female bonobos are poorly understood. To identify the timing of natal emigration relative to puberty, I measured urinary estrone conjugates (E_1C) and pregnanediol glucuronide (PdG) in wild female bonobos and observed their copulatory interactions with mature males. Data were collected from eleven nulliparous female bonobos before/after natal emigration at Wamba, Democratic Republic of the Congo. The results showed that any ovulatory signals implied by a sustained rise of PdG levels were not detected until at least one year after emigration, whereas E_1C 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 can benefit them to postpone high energetic costs for first reproduction until they become familiar with the new group or to allocate more time for seeking better groups before they settle down.

2. Introduction

Puberty is a stage of dramatic biological changes that allow one to become physiologically capable of reproduction (Bronson and Rissman 1986; Dorn and Biro 2011; Fortenberry 2013). It includes physical growth, sexual maturation, cognitive development, and social and behavioral changes in the process until individuals become adults (e.g., Forbes and Dahl, 2010; Sisk and Zehr 2005; Smith et al. 2013; Steensma et al. 2013). Complex mechanisms of puberty and its sex-specific functions have been clarified by many hormonal studies in humans (Berenbaum and Beltz 2011; Bordini and Rosenfield 2011; Campbell 2006). Hormonal analysis has been also widely used to trace developmental processes in non-human mammals (Bercovitch and Ziegler 2002; Bronson and Rissman 1986; Wallen and Zehr 2004), by referring to extensive data on endocrinological correlates of development in humans. Current non-invasive methods have enabled me to monitor hormonal profiles of immature individuals sampled in wild populations (e.g., Gesquiere et al. 2005; Marty et al. 2015; Putman et al. 2019; Wolf et al. 2018). Field studies on hormones and behaviors may contribute to a better understanding of backgrounds and motivations for pubertal events that have been incorporated over evolutionary time (Gluckman and Hanson 2006).

Natal dispersal can be an important pubertal event in an individual’s life history (Dobson 1982). In most social mammals, members of one or both sexes transfer out of their natal group to avoid local resource competition (Koenig 2002; Moore and Ali 1984) or inbreeding (Clutton-Brock 1989; Pusey 1987; Rood 1987). As individuals near maturity, they may be evicted by same-sex residents due to limited resources (e.g., Ochiai and Susaki 2006; Pusey and Packer 1987; Whiteside et al. 2011) or voluntarily leave their natal groups to seek unrelated mates elsewhere (e.g., Honer et al. 2007; Stokes et al. 2003; Walker and Pusey 2020). Natal dispersal often occurs with pubertal changes such as the onset of copulative behaviors, secondary sexual characteristics, and estrous signs (e.g., male spotted hyaena, *Crocuta crocuta*, Holekamp and Smale 1998; female black-crested gibbons, *Nomascus noncolor*, Hu et al. 2018; male mountain gorillas, *Gorilla beringei*, Stoinski et al. 2009). Several hormonal studies have reported that the elevation of reproductive hormones occurs before or around the time of the dispersal event (e.g., male ground squirrels, *Spermophilus beldingi*, Nunes et al. 1999; male European badger, *Meles meles*, Woodroffe et al. 1993; male yellow baboons, *Papio cynocephalus*; Onyango et al. 2013; female tammar wallabies, *Macropus eugeni*: Williams et al. 1998; female owl monkeys, *Atous azarae*, Corley et al. 2017). However, pubertal influences on natal dispersal do not necessarily apply to all species (e.g., male white-faced capuchins, *Cebus capucinus*, Jack et al. 2014; female northern muriquis, *Brachyteles hypoxanthus*, Strier and Ziegler 2000).

In chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), dispersal is biased toward females (Furuichi et al. 2015) and unlikely to be caused by overt eviction (Pusey 1990). These females typically emigrate from the natal group to another group as nulliparous status (Gerloff et al. 1999; Goodall 1986; Nishida 1979; Kano 1982). However, the stage of sexual development at the moment of natal emigration considerably varies between the closest species. In most cases, female chimpanzees exhibit the swelling of the perineum skin (sexual swelling) and copulate with mature males prior to emigration (Nishida 1990; Pusey 1990; Stumpf et al. 2009). By contrast, female bonobos still do not have sexual swelling and rarely show copulation with mature males prior to emigration (Hashimoto, 1997; Sakamaki et al., 2015). In fact, female bonobos transfer out of their natal group at an earlier age (6–8 years, Lee et al. 2019; Sakamaki et al. 2015) than do female chimpanzees (11–13 years, Witting and Boesch 2019; Nakamura 2015; Stumpf et al. 2009; Walker et al. 2018).

This age difference between the *Pan* species can be due to the different costs of female transfer for each species. Compared to resident conspecifics, dispersers often face greater fitness costs, such as predation risk, energetic loss, and social stress (Alberts and Altmann 1995; Isbell and van Vuren 1996; Maag et al. 2019). Immigrant females may suffer a competitive disadvantage in conflicts with resident females due to limited local resources (e.g., Dittus 1986; French and Inglett 1989; Riveros et al. 2017; Watts 1991). For example, female chimpanzees can be hostile toward new immigrant females due to competition over food resources (Kahlenberg et al. 2008b; Pusey et al. 2008; Townsend et al. 2007) while female bonobos can be tolerant toward unfamiliar immigrant females so as to share food patches and exchange affiliative interactions (Idani 1991; Sakamaki et al. 2015). Therefore, the potential costs associated with the process of social integration into the established group may be smaller in bonobos than in chimpanzees, thereby reducing the developmental threshold for their decision on natal emigration.

Age is a typical indicator of individuals' life stages, but developmental rates vary considerably among species. Bonobos are characterized by developmentally delayed expressions of morphological, cognitive, and behavioral traits in comparison with chimpanzees (e.g., Boughner and Dean 2008; Kuroda 1989; Rosati and Hare 2012; Wobber et al. 2010). However, in captivity, female bonobos can reach dull adult bodyweight at an earlier age than female chimpanzees (Leigh and Shea 1996). Additionally, captive female bonobos can give birth to their first infants at a younger age than female chimpanzees (Parish 1996), but other data suggest that the onset of reproductive careers may be at a similar age between them (de Lathouwers and van Elsacker 2005). Furthermore, one hormonal study provided evidence that female bonobos reach puberty at a younger age than female chimpanzees by comparing the ontogenetic changes in urinary testosterone levels between the *Pan* species (Behringer et al. 2014). This previous study suggests that the earlier onset of puberty in female bonobos may be in line with their younger age of natal emigration compared to female chimpanzees. However, I cannot examine the pubertal correlates of natal emigration without corresponding hormonal and behavioral data in wild female bonobos.

My objectives were to identify the stage in sexual development at natal emigration in wild female bonobos. Puberty starts with a reawakening of the hypothalamic-pituitary-gonadal (HPG) axis: secretion of gonadotropin-releasing-hormone (GnRH) increases which activates the pituitary to release luteinizing hormone (LH) and follicle-stimulating hormone (FSH) (Plant and Barker-Gibb 2004; Styne 1994; Winter et al. 1978). In females, the rise in LH and FSH stimulates the ovaries to produce an increasing amount of estradiol, which is responsible for the development of secondary sexual characteristics (Jenner et al. 1972; Pinyerd and Zipt 2005; Terasawa and Fernandez 2001). Progesterone levels remain low in the early stage of puberty, but after menarche, elevating amount is generally indicative of ovulation (Apter 1980; Lee et al. 1976; Zhang et al. 2008). In this study, I examined whether the hormonal and behavioral changes of puberty precede the timing of natal emigration in female bonobos. I determined urinary estrone conjugates (E_1C) and pregnanediol glucuronide (PdG) levels (major urinary metabolites of estrogens and progesterone known to reflect ovarian function in the bonobos, e.g., Heistermann et al. 1996; Shimizu et al. 2003b; Wright et al. 1981) collected from nulliparous female bonobos before/after natal emigration. I also recorded observable data of their copulatory interactions with mature males.

3. Methods

3-1. Study site and subjects

This study was conducted at Wamba, in the northern sector of the Luo Scientific Reserve, Democratic Republic of the Congo, where long-term field research of wild bonobos has been conducted since 1974 (Furuichi et al. 2012; Kano 1992). Artificial provisioning was initially used for behavioral observations until 1996, when field research was interrupted by war in the DRC (Hashimoto et al. 2008). This provisioning was abolished in 2003, when research was resumed. Data were collected from two habituated bonobo groups, the “E1” and “PE” groups, during six different periods (three to six months) between November 2014 and March 2019. Bonobos were followed from where their night beds were (usually around 06:00) until they made new night beds (usually around 17:00; Mulavwa et al. 2010). I recorded the presence of identified bonobos on a daily basis to follow demography such as birth, death, emigration, and immigration of individuals (Sakamaki et al. 2015). During the study period, the E1 and PE groups included 29–37 and 17–25 independent individuals, respectively. Parous females of the study groups have all consisted of immigrant females (Hashimoto et al. 2008; Kano 1992; Sakamaki et al. 2015).

I focused the investigation on eleven nulliparous females who had emigrated from their natal groups (Table 3-1). When females immigrated into other neighboring groups or disappeared with good health at last seen, I considered them as having emigrated. In Wamba, so far, all female bonobos have transferred out of their natal group before first parturition (Hashimoto et al. 2008; Sakamaki et al. 2015). During my study periods, natal females all dispersed from their natal group before at least est. 10.8 years old. My subjects comprised of seven natal females that emigrated from the study group, three non-natal females that immigrated into the study group, and one female that transferred between groups. I classified them into “emigrant (prior to emigration)” and “immigrant (posterior to immigration)” based on demographical records. I should also note that the four immigrants transferred directly from their natal group, the “PE” and “PW” groups, where all bonobos had been identified since 2011 and 2012, respectively (Sakamaki et al. 2018). Thus, the date of their immigration coincides with that of their emigration from the natal group.

3-2. Behavioral observations

All observable events of copulation were recorded ad libitum while following bonobos of the E1 and PE groups for 2655 hours over 339 days (7.83 ± 2.46 hours per day) and 1035 hours over 143 days (7.23 ± 2.40 hours per day), respectively. Copulation was defined as mounting with the insertion of the penis to the vagina between females and males, distinguishing from other genital contact without penile erection, insertion, and thrusting movement (Hashimoto 1997). Since previous works have reported that male bonobos start to reproduce at the age of seven years (Thompson-Handler 1990), I focused on copulation with adolescent and adult males (mature males) in the group. In total, I collected 238 copulatory interaction events.

Bonobos live in fission-fusion grouping dynamics where the members of a sub-group (party) changes fluidly and flexibly (Kuroda 1979; White 1988). When group members split into two or more temporary parties, the largest party was followed whenever possible. I recorded a “one-hour party” in which party membership was determined by all individuals present from the beginning of every hour to the end of each hour interval of following bonobos (Hashimoto et al. 2001; Mulavwa et al. 2008). I counted whether or not a given subject copulated with mature males for each one-hour party segment she was observed.

3-3. Urinary sample processing

I and local assistants non-invasively collected 891 samples from identified subjects that had urinated on the leaves of vegetation using filter papers (Whatman #1 with 5.5 cm in diameter) (Mouri and Shimizu, submitted). We did not collect urine contaminated by soil, feces, fruit juice, or urine from other individuals. Within the day of collection, I completely dried the urine adsorbed filter papers in a dry box containing silica gel for one week (Knott 2005). I stored the dried filter papers in the dark at room temperature (20 to 28°C) for less than six months at the study site, then transported them to the Primate Research Institute at Kyoto

University in Japan and stored at –20°C.

3-4. Hormonal assays

I and another researcher extracted from the filter papers with 1.5 ml deionized water by shaking them on the reciprocal shaker (TAITEC, Japan) for two hours. Previous studies had confirmed that the PdG, E_1C, and creatinine (Cr) concentration of the extracts from urine-absorbed filter papers were highly correlated with the concentrations of the original urine samples up to one year at room temperature (Mouri and Shimizu submitted). After urine extraction, we measured the Cr concentration with Jaffe reaction methods to use as the index of urinary steroid metabolite levels (Taussky 1964). I measured determined the E_1C and PdG concentrations in duplicate from 779 urinary samples, using enzyme immunoassays (EIAs) validated in filter paper extracts from chimpanzees' urine samples (Mouri and Shimizu submitted).

I used polyclonal antibodies raised against estrange-3-glucuronide bovine serum albumin (BSA) (FKA334E Cosmo Bio, Japan), pregnanediol-3-glucuronides BSA (FKA 224E Cosmo Bio, Japan), and horseradish peroxide-conjugated steroid derivatives (Cosmo Bio, Japan) for the EIAs. Cross-reactivity information of the antibodies against E_1C and PdG was provided by the manufacturer (Cosmo Bio, Japan). The E_1C antibody cross-reacted 100% for estrone-glucuronide, 2.5% for estradiol-3-glucuronide, and < 1% for other steroids. The PdG antibody cross-reacted 100% for pregnanediol-3-glucuronide, 16% for 20α-OH-progesterone, 2.3% for progesterone, < 1% for other steroids. The sensitivities of the assay at 90% binding were 5.3 pg/ml and 1.4 ng/ml for E_1C and PdG, respectively. Parallelism was checked using constant dilutions of filter paper extracts from three different bonobos, and recovery was tested by adding known amounts of E_1C and PdG standards to the samples (Ryu, 2017). The serially diluted extracts depicted parallel displacement curves against standard curves for E_1C and PdG, and ANCOVA tests confirmed that there was no serious violation of parallelism between the diluted samples and the standards (n = 3x4; p = 0.155 to 0.337 for E_1C and 0.255 to 0.730 for PdG). The recovery tests showed high regression coefficient values (n = 3x4; E_1C: $y = 0.99x + 0.01$, $r^2 = 0.985$; PdG: $y = 0.99x - 2.5$, $r^2 = 0.967$), which suggests that E_1C and PdG were successfully recovered in assays.

I excluded all low-concentration samples with an intra-assay coefficient of variations (CV) higher than 20%, and I re-assayed the other high concentration samples with a CV over 20%. The intra-assay CVs in my final data set, which included 779 urine samples, were 5.94% for E_1C and 6.54% for PdG. Inter-plate CVs were 12.5% and 13.9% for E_1C (n = 42) and 19.5% and 19.0% for PdG (n = 45) at high and low controls, respectively.

3-5. Ovulation detection

To determine the occurrence of ovulation (or the corresponding onset of luteal phase), I used the criteria of PdG-defined ovulation described in previous studies on bonobos (Douglas et al. 2016; Heistermann et al. 1996). Ovulation was defined as a sustained rise in PdG levels above two standard deviations (SDs) from the baseline, which was determined by the running mean of PdG levels for three or more days within the ten days preceding each data point (Ryu 2017). When the baseline was not established due to less than two data points within the preceding ten days, I did not assess PdG-defined ovulation. Furthermore, the mean PdG levels of the ten days following ovulation should be higher than that of the baseline. This is because the previous study in adult female bonobos in the wild has presented the luteal phase as 9.5 ± 1.2 days, calculated from the day of ovulation to the first day of observed menstruation (Douglas et al. 2016). When both urinary PdG and E_1C were continuously highly elevated, I considered it as a conceptive period (Heistermann et al. 1996; Shimizu et al. 2003a).

3-6. Statistical analyses

To investigate pubertal changes in urinary E_1C levels and copulation rates (a) prior and (b) posterior to natal emigration in female bonobos, I ran four generalized linear mixed models (GLMMs), using the package function "lme4" (Bates et al. 2015) of R software 3.6.1 (R Core Team 2019). GLMMs take account of the unbalanced repeated measure (Cnaan et al. 1997), thereby allowing me to include multiple data points from the same female. I nested the female identity as a random variable in the models to avoid pseudo-replication. Data points for E_1C were non-normal distributions, positive and skewed toward larger levels, and thus, log-transformed E_1C levels as the response variable in the model (GLMM 1) fitted with a Gaussian distribution (Baayen 2008). I excluded sixty-four urine samples collected during an estimated conception, regardless of the outcome of abortion or parturition, from the model analysis. Further, I included binary values between one-hour party segments with copulation and those without copulation that were fitted with a binomial error structure and logit-linked function as the response variable in the other model (GLMM 2) (Zuur et al. 2009). The binary values were aggregated for a monthly interval and linked using the "cbind" function in the model.

I calculated the relative day of all data points based on the date of natal emigration in female subjects. For example, if a urine sample or an observation was collected at 100 days before emigration in a given female, the data were pointed at –100 days relative to emigration. In the model analysis for emigrants and immigrants, I used the data collected during (a) –1000 to 0 days and (b) 0 to 1000 days relative to the emigration, respectively. As the main predictor in the models, I included the relative time (day or month) prior and posterior to the date of natal emigration, separately. Since the time-related changes in E_1C levels and copulation rates can be non-linear (i.e., quadratic curve), I also incorporated the squared value of the relative time as the predictor variable to achieve a reliable model (e.g., Kulik et al. 2016; Langos et al. 2013). To avoid collinearity between the linear and quadratic values, I centered (transformed) the relative time of each data point by subtracting the mean value of all the data points (Robinson and Schumacker 2009). Prior to running the models, I *z*-transformed all predictor variables to a mean of zero and a SD of one.

I used Akaike's information criterion (AIC) for model selection (Burnham and Anderson, 2002) and selected GLMM l, which had a smaller AIC value between the quadratic regression and linear regression models. For GLMM 1a and 2a in emigrant females, AICs were smaller in the linear regression models, whereas for GLMM 1b and 2b in immigrant females, they were smaller in the quadratic models (Table S3-2). To check the assumptions of the quadratic regression models, I calculated variance inflation factors (VIF, Quinn and Keough 2002), using the "vif" function of the "car" package (Fox and Weisberg 2018), which indicated that collinearity between predictor variables was not an issue (maximum VIF = 1.09). I also ran likelihood ratio tests (LRTs, Dobson and Berntt 2008) to determine the overall statistical significance of the AIC-selected models by comparing these fits with that of the respective null models including only the random effects.

3-7. Ethical statement

This study was approved by the Ministry of Scientific Research and the Center of Research for Ecology and Forestry in Democratic Republic of Congo. This study was also conformed to the Guidelines for Field Research of Wild Non-Human Primates established by the Primate Research Institute of Kyoto University. Urinary sample collections and behavioral observations were conducted non-invasively and with care so as not to affect the behavior and environment of the wild bonobos and other animals. The authors declare that they have no conflict of interest.

4. Results

Any ovulation signs defined with urinary PdG levels were not detected until at least one year after natal emigration, although I could not examine a whole period of each subject due to my fragmentary samples (Fig. 3-1). For emigrant females, PdG was seen to fluctuate at a low level, while E_1C levels were more stable. On the other hand, for immigrant females, comparatively large fluctuations in PdG and E1C levels were observed. Overall, I identified five instances of ovulation; three of them appeared to be non-conceptive ovulatory cycles (e.g., Fig. 3-2a); the other two were likely to be conceptive ovulatory cycles (e.g., Fig. 3-2b). Further, I estimated four instances of conception based on the continuous elevation of both PdG and E_1C levels, one of which was considered to have resulted in abortion because the reproductive hormone levels then decreased. First parturition was confirmed in immigrant females at 2.6–3.5 years after their natal emigration.

GLMM 1a (linear regression model) for urinary E_1C levels in emigrant females was better than its null model ($df = 1, \chi^2 = 72.3, p < 0.001$). The relative day prior to natal emigration had a positive correlation with E_1C levels (Table 3-2a; Fig. 3-2a). GLMM 1a indicates that the E_1C levels increased close to the time of emigration. In addition, GLMM 1b (quadratic regression model) for E_1C levels in immigrant females was better than its null model ($df = 2, \chi^2 = 75.7, p < 0.001$). The relative day posterior to natal emigration had a positive correlation with E_1C levels while its squared value had a negative correlation (Table 3-2b; Fig. 3-2b). GLMM 1b indicates that E_1C levels increased after emigration and gradually came to close to a plateau. My results showed that the increase in E_1C levels preceded the event of natal emigration.

GLMM 2a (linear regression model) for copulation rates in emigrant females was better than the null model ($df = 1, \chi^2 = 22.4, p < 0.001$). The relative month prior to emigration had a positive correlation with the probability of copulation (Table 3-3a; Fig. 3-3a). GLMM 2a indicates that copulation rates increased prior to the time of emigration. In addition, GLMM 2b (quadratic regression model) for immigrant females was better than the respective null models ($df = 2$, $\chi^2 = 13.1$, $p = 0.001$). The relative month posterior to emigration had a positive correlation with the probability of copulation, while its squared value had a negative correlation (Table 3-3b; Fig. 3-3b). GLMM 2b indicates that copulation rates reached a vertex at the midpoint of time after emigration. My results showed that the onset of copulative behaviors preceded the event of natal emigration.

5. Discussion

This study implies that natal emigration can be associated with the time at which female bonobos undergo an endocrinological change of puberty. Urinary E_1C levels increased from before emigration and continued to increase thereafter until coming close to a plateau. This gradual increase in E_1C levels before and after emigration may reflect the increasing amount of ovarian estradiol production during puberty (Terasawa and Fernandez 2001; Winter et al. 1980), whereas the rise of urinary PdG levels induced by the occurrence of ovulation was not found before emigration. In the early stage of puberty in human girls, even if secondary sex characteristics have appeared, follicular development stimulated by rising levels of estradiol fails to reach the ovulatory phase developing corpus luteum (Apter 1980; Lee et al. 1976; Zhang et al. 2008). Subsequently, the further elevation of ovarian estrogen secretion triggers ovulation through LH surge, and normal ovulatory cycles become established by developed feedback mechanisms of the HPG axis (Bordini and Rosenfield 2011; Peper et al. 2010; Rosewir and Millar 2009). Thus, female bonobos can be considered to transfer out of their natal group at the early stage of puberty with the absence of ovulation.

This study matches the expectation that natal emigration precedes a time when the risk of inbreeding occurs (Clutton-Brock 1989; Honer et al. 2007; Lehmann and Perrin 2003; Pusey 1987). The hormonal findings suggest that normal ovulatory cycles may be not established until at least one year after natal emigration in female bonobos. A few copulatory interactions with mature males in the natal group were observed in five out of six emigrant females but were unlikely to be connected to fertilization. In addition, copulation rates increased after emigration and reached a vertex at the midpoint in time. Although it is difficult to directly test the adaptive strategy of female transfer against inbreeding depression, natal emigration in female bonobos may be correlated with the time at which they acquire sexual receptivity during puberty. Further, outbreeding motivation can play a proximate role in inbreeding avoidance fir influencing individual dispersal decisions (Corley et al. 2017; Sterck et al. 2005; Stokes et al. 2003; Vigilant et al. 2015). More intensive behavioral sampling on pubertal female bonobos during intergroup encounters may allow me to examine their mating preference for neighboring group males compared to natal group males.

Female bonobos appeared to experience a prolonged time between natal emigration and sexual maturation. Although urinary E_1C levels increased from before emigration, PdG-estimated ovulation was delayed from the emigration. My results in female bonobos partially resemble those in a previous study of female northern muriquis (Strier and Ziegler 2000) in that dispersal is biased toward females as well in the *Pan* species (Strier et al. 2015). This hormonal study revealed that female muriquis transferred out of their natal group and into new groups prior to the onset of ovulatory cycling (Strier and Ziegler 2000). Strier and Ziegler (2000) have suggested that females may benefit from early emigration relative to the time of sexual maturation by postponing the energetic costs of lactation and gestation until they become familiar with the new group, citing a review paper on the biology of puberty (Bronson and Rissman 1986). Nutritional deficiency and social stress associated with social integration into an unfamiliar group could result in delaying reproductive careers, even if females leave their natal group at sexual maturation. This hypothesis may predict that later emigrant females experience a reproductive delay compared to early emigrant females and that natal females (i.e., non-dispersing females) give birth to first infants earlier than immigrant females do. For example, in chimpanzees, immigrant females give birth to their first infants at a later age than natal females (16.2 versus 13.7 years) presumably due to the relatively higher competition over food resources (Walker et al. 2018). Female bonobos might take this conceivable strategy of early emigration to smooth beginning of their reproductive careers when they become physiologically capable of fertility.

Another reason that female bonobos might take this strategy is to allow more time for them to find a better group they will settle down with. Nulliparous female bonobos tend to visit several groups through intergroup encounters until they settle into a specific group (Kano 1992; Sakamaki et al. 2015); such temporary visits are also seen in chimpanzees (Boesch and Boesch-Ackermann 2000; Goodall 1986; Nishida et al. 2003) and northern muriquis (Strier et al. 2015). If the female reproductive rate is variable across groups, group choice based on food availability and male quality can be important to dispersed females (Bowler and Benton 2005; Jack and Fedigan 2009). For example, female Thomas langurs (*Presbytis thomasi*) tend to transfer into smaller groups with lower food competition, when the males of their group are no longer good protectors for infanticide (Sterck et al. 2005). However, in the current study, four female subjects who had immigrated from their natal groups into the E1 group were not observed to visit other groups for a temporary period. This may be because there are fewer opportunities per year for encounters with neighboring groups in the E1 group compared to the PE and PW groups (Sakamaki et al. 2018), and the Ekalakala and Kokoalong groups at the Koolopori bonobo reserve (Lucchesi et al. 2020). Although the group difference in the female reproductive rate is unknown in bonobos, I would like to note that the prolonged period between natal emigration and sexual maturation might allow female bonobos to experience more groups for the group choice.

Female chimpanzees might have a restriction of the stage in sexual development at immigration into the established group. The “swelling passport” hypothesis as a tool of immigrant females use to derive the service of male protection in preventing intensive aggression from resident females has been proposed in chimpanzees (Kahlenberg et al., 2008a; Nishida, 1979; Pusey, 1979). Even though the entry of outgroup females is basically beneficial for male reproduction, immigrant female chimpanzees may need to advertise sexual receptivity so as to receive male protective services. Adolescent female chimpanzees are described as exhibiting a longer period of sexual swelling compared to adult females (Graham 1972; Wallis 1997; Kahlenberg et al. 2008a). Their prolonged swelling might play a role in associating with males for a longer period (Kahlenberg et al., 2008a). By contrast, given that female bonobos can be integrated into the established group without the sexual swelling, this swelling passport hypothesis is unlikely to apply to bonobos, where resident females are comparatively tolerant toward immigrant females. Immigrant female bonobos tend to allocate their more efforts to form affiliative relationships with older resident females rather than with resident males (Furuichi 1989; Idani 1991). Nonetheless, sexual swelling is also prolonged in adolescent female bonobos (Furuichi 1987; Ryu et al. 2015), and it functions to attract not only males but also females (Ryu et al. 2015). Thus, even though the development of the perineum skin is not necessarily required for female transfer in bonobos, the prolonged swelling might contribute to facilitating their approach to resident females. It will be interesting to examine the behavioral and social changes in young females corresponding to their anogenital swelling development.

This study provides the first description of reproductive hormone profiles and copulatory behaviors in wild nulliparous female bonobos before and after leaving their natal groups. My results indicate that the activation of ovarian estrogen secretion and the onset of copulation during the early stage of puberty may underlie the timing of natal emigration in female bonobos. In spite of my small sample size, the findings indicate that the ovulatory cycle in nulliparous female bonobos is likely to be developed after natal emigration. Indeed, the high tolerance of female bonobos toward immigrant females compared to that of female chimpanzees might enabled natal emigration at a younger period, when they are still vulnerable to predators and are poorly competitive. This study emphasizes the need for further investigation of the advantages involved with early emigration relative to sexual maturation. The key to a better understanding of this pubertal social event may be an integrated view of the developmental stage and socio-ecological conditions.

Table 3-1. Information of nulliparous emigrant and immigrant females between 2014 and 2019 in the E1 and PE groups at Wamba, DRC

ID	Birthdate	Group[c]	Natal emigration		First parturition		Urine
			Date	Age (years)	Date	Age (year)	sample[d]
Emigrant							
Mazy	2012/11/07–08	PE to ?	2019/06/27	6.7			44
Fua	2010/12/29–2011/01/06	E1 to ?	2018/03/21	7.2			73
Otoko	2010/12/24–2011/01/11	E1 to ?	2017/07/04	6.5			83
Yume	2009/10/06–07	E1 to ?	2016/08/01	6.8			71
Pipi	2009/01/01~2009/06/30[b]	PE to ?	2016/08/06	7.1~7.6			31
Natsuko	2009/05/10–15	E1 to ?	2015/11/06	6.5			37
Nadir	2008/9/4–2008/9/9	E1 to ?	2015/9/05–15	7.0			26
Sachi[a]	2008/07/01~2009/06/30[b]	PE to E1	2015/11/22	6.4~7.4			19
Immigrant							
Debby	2009/01/01~2009/12/31[b]	PW to E1	2016/08/06	6.6~7.6			80
Sachi[a]	2008/07/01~2009/06/30[b]	PE to E1	2015/11/22	6.4~7.4	2019/03/17–04/06	9.7~10.7	120
Ichiko	2007/01/01~2008/12/31[b]	PE to E1	2014/10/02	5.8~7.8	2017/05/09–05/15	8.4~10.4	124
Puffy	2003/01/01~2005/12/31[b]	PE to E1	2013/10/12	7.8~10.8	2016/10/05–19	10.8~13.8	71

[a] Same female.

[b] Birth estimation based on body size at the first identification.

[c] Transferred from natal group to another group.

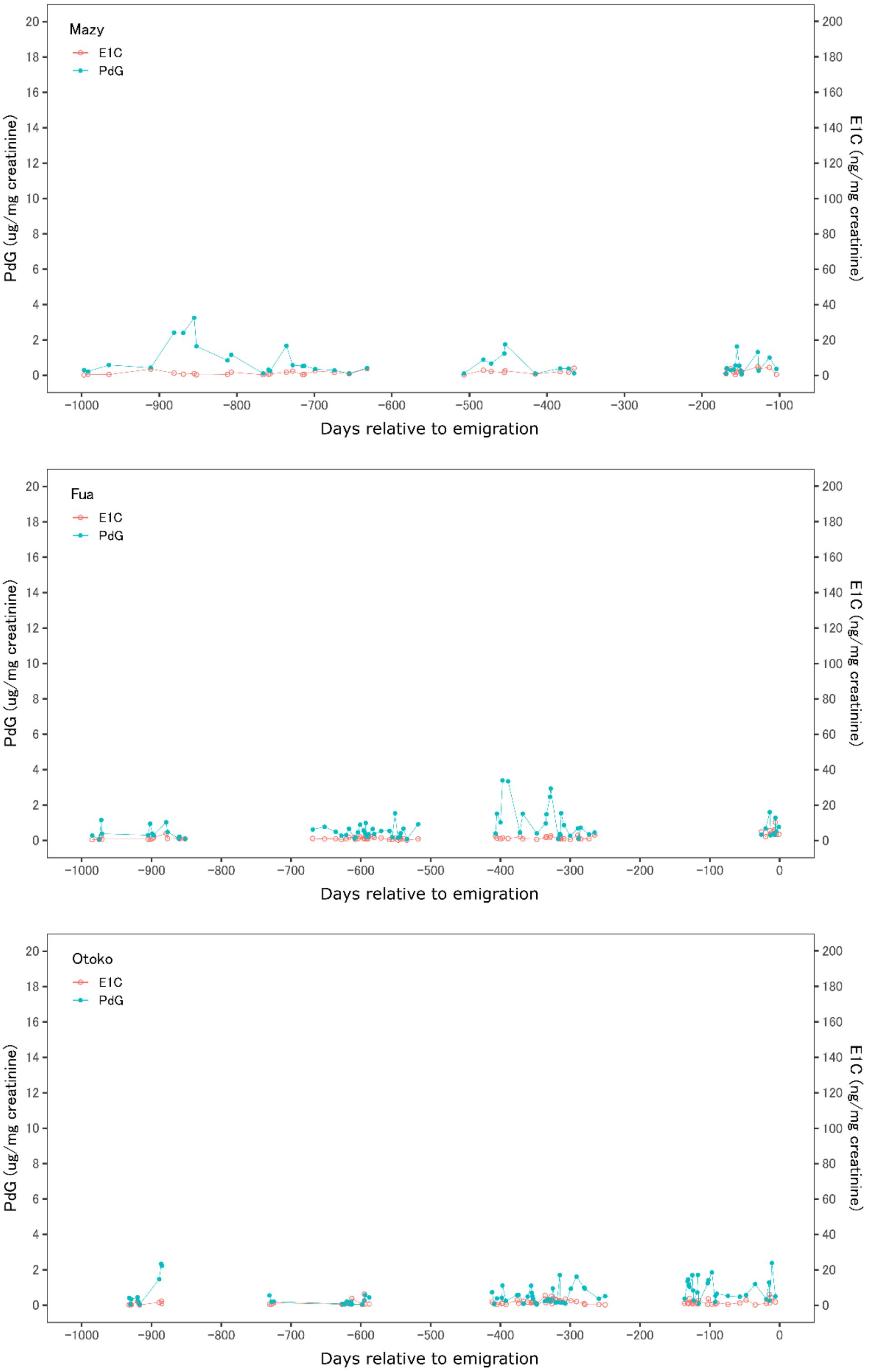
[d] Number of urine samples in which both E_1C and PdG levels were determined.

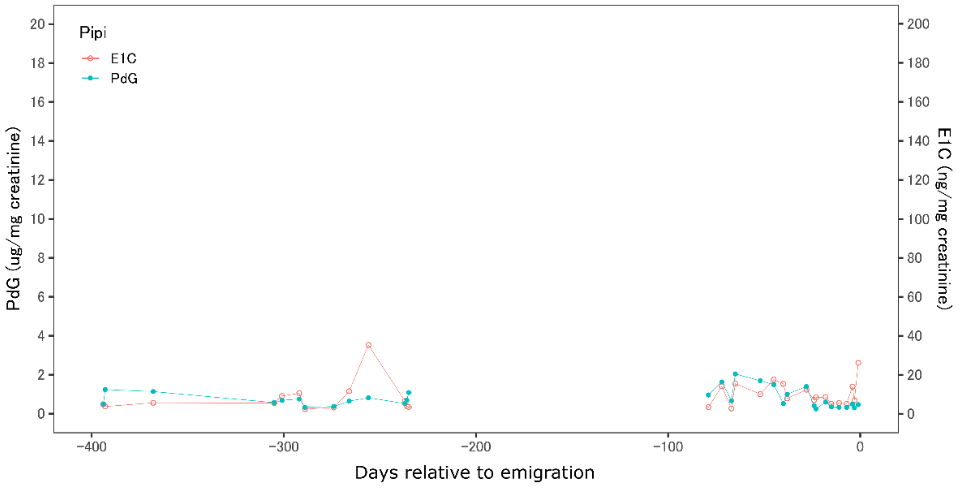
Table S3-2. Model selection with Akaike's information criterion (AIC)

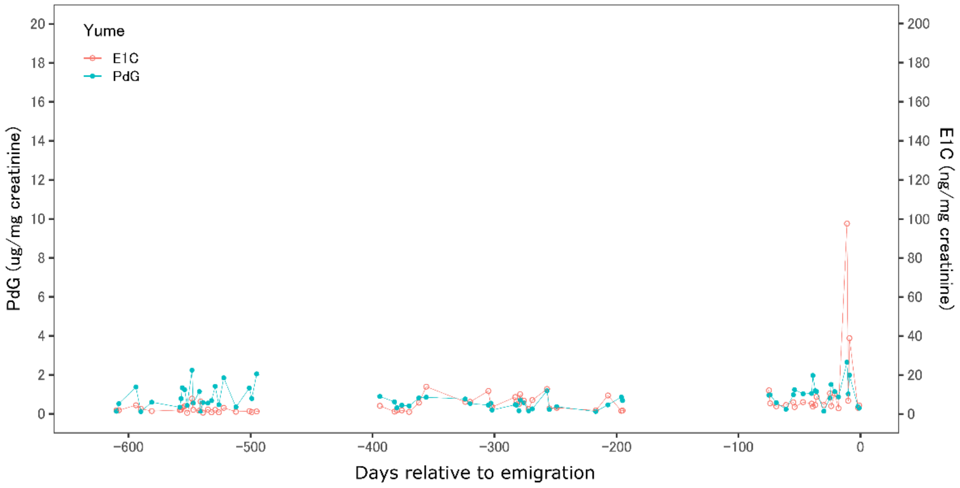
Order	***df***	GLMM 1s (E_1C)		GLMM 2s (Copulation)	
		AIC	**ΔAIC**	**AIC**	**ΔAIC**
(a) prior to emigration					
Quadratic regression model	5	918.3	0	75.9	0
Linear regression model	**4**	**916.6**	**–1.7**	**74.6**	**–1.3**
Null model	3	981.6	65.0	95.0	20.4
(b) posterior to emigration					
Quadratic regression model	**5**	**804.5**	**0**	**263.6**	**0**
Linear regression model	4	804.7	0.2	269.1	5.5
Null model	3	867.6	63.1	272.6	9

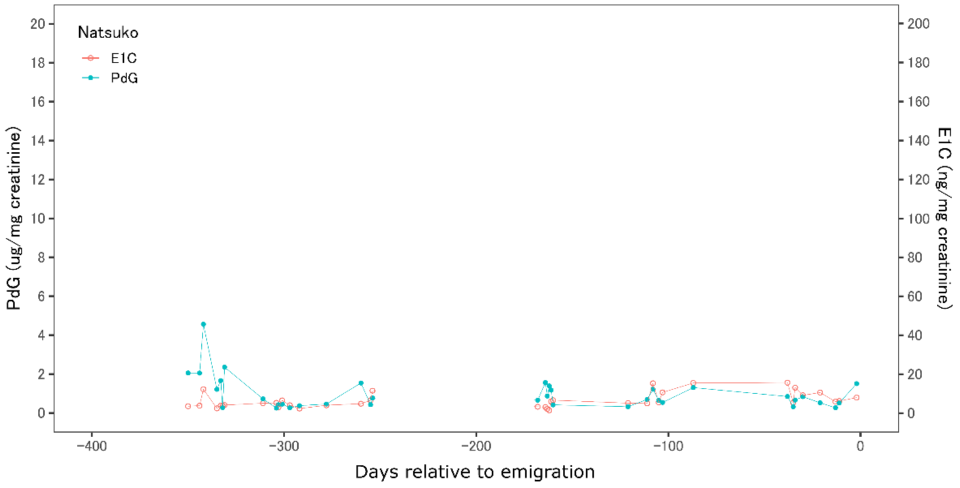
Smaller AIC models are indicated in bold.

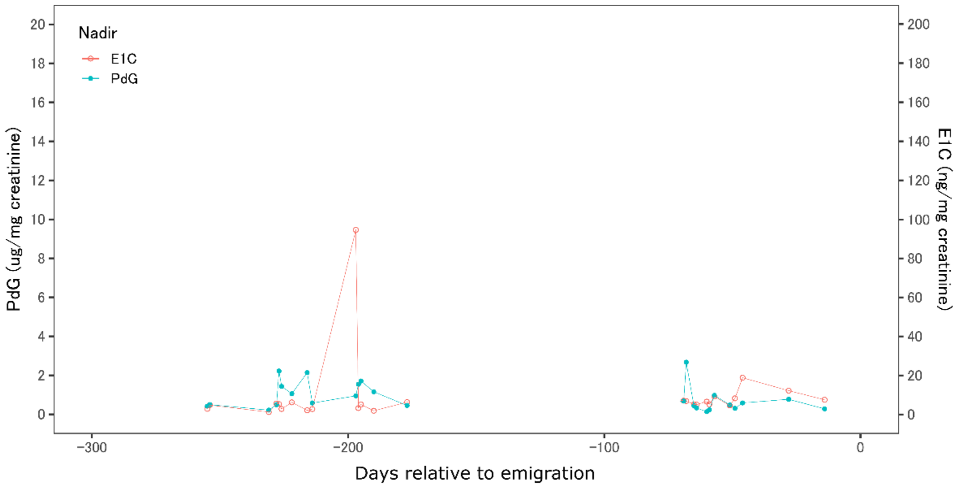
Fig 3-1. Hormonal profiles in urinary PdG and E_1C levels relative to the date of natal emigration for each female ($N = 11$)

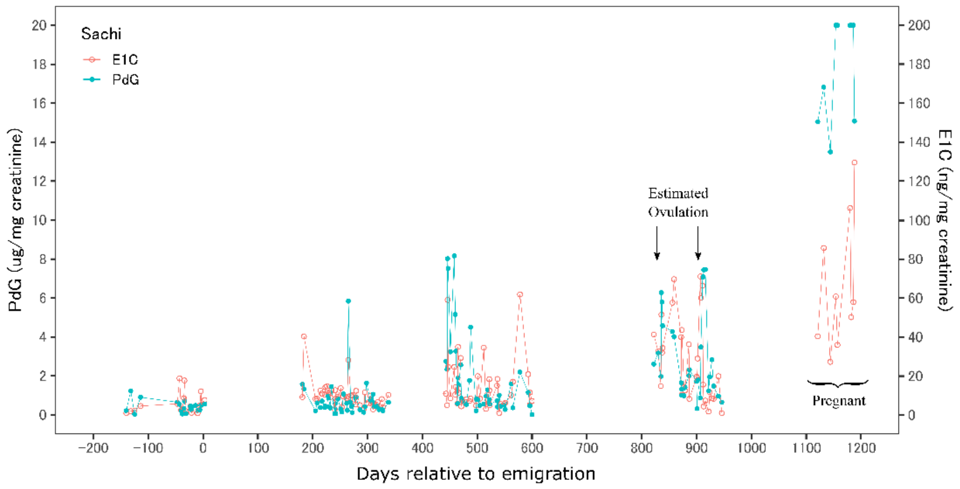


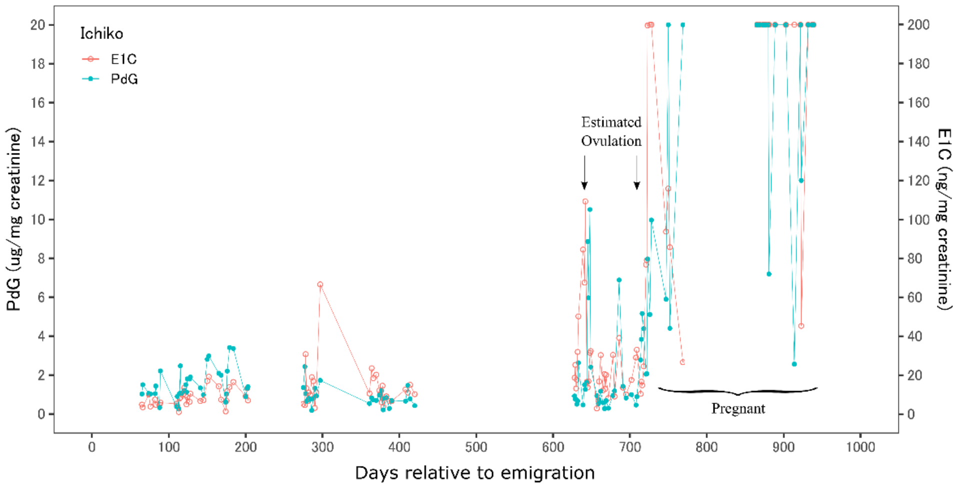

Pipi
E1C
PdG
PdG (ug/mg creatinine)
E1C (ng/mg creatinine)
0
2
4
6
8
10
12
14
16
18
20
0
20
40
60
80
100
120
140
160
180
200
−400
−300
−200
−100
0
Days relative to emigration

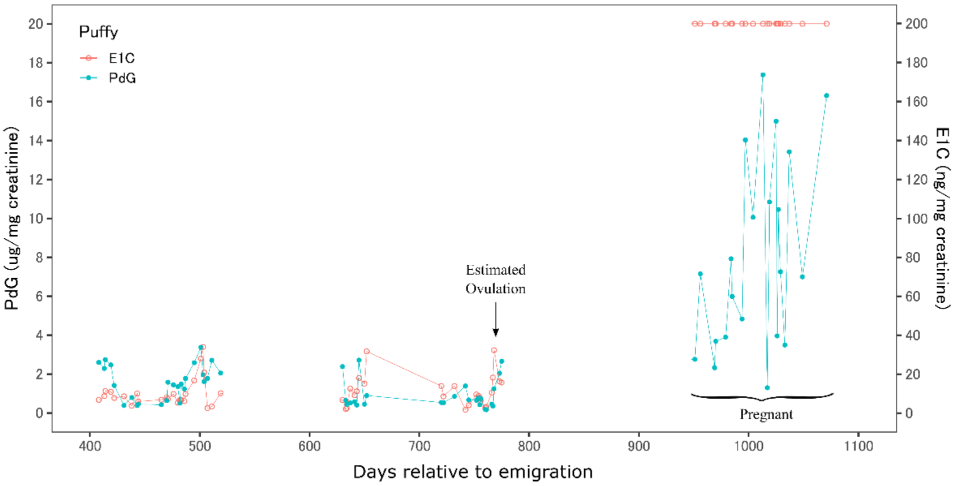

Yume
E1C
PdG
PdG (ug/mg creatinine)
E1C (ng/mg creatinine)
0
2
4
6
8
10
12
14
16
18
20
0
20
40
60
80
100
120
140
160
180
200
−600
−500
−400
−300
−200
−100
0
Days relative to emigration


Natsuko
E1C
PdG
PdG (ug/mg creatinine)
E1C (ng/mg creatinine)
0
2
4
6
8
10
12
14
16
18
20
0
20
40
60
80
100
120
140
160
180
200
−400
−300
−200
−100
0
Days relative to emigration


Nadir
E1C
PdG
PdG (ug/mg creatinine)
E1C (ng/mg creatinine)
0
2
4
6
8
10
12
14
16
18
20
0
20
40
60
80
100
120
140
160
180
200
−300
−200
−100
0
Days relative to emigration

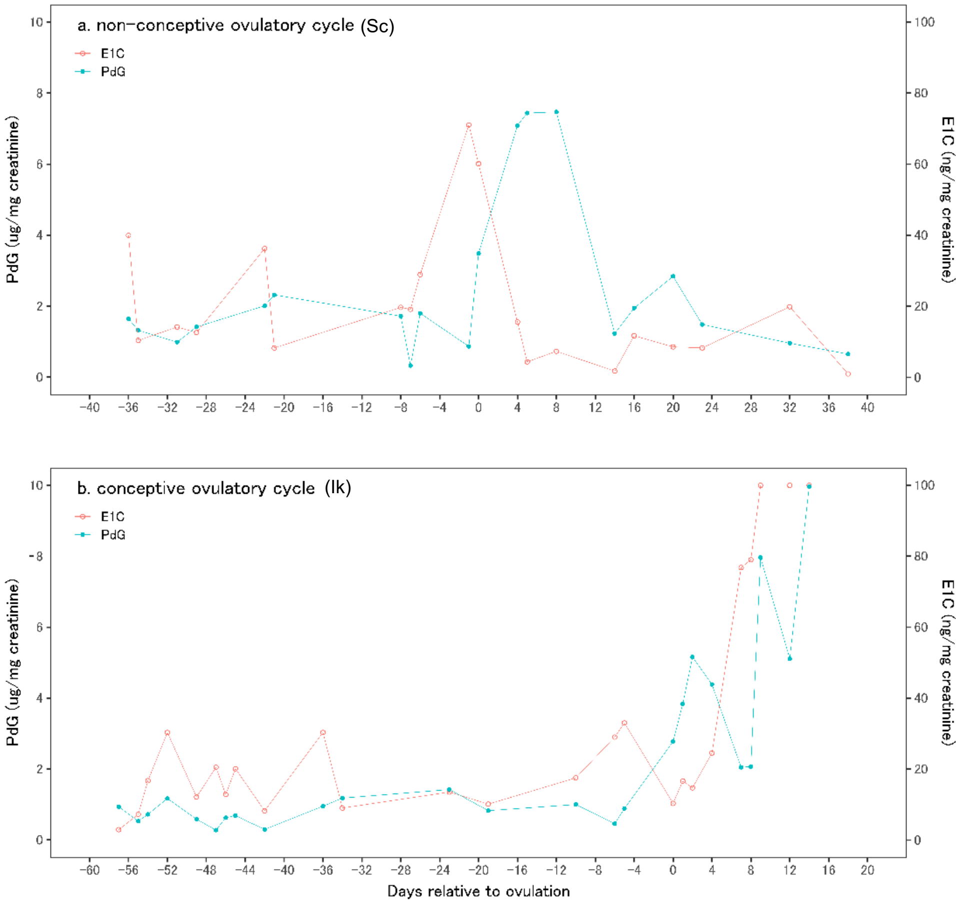

Sachi
E1C
PdG
Estimated
Ovulation
Pregnant
PdG (ug/mg creatinine)
E1C (ng/mg creatinine)
0
2
4
6
8
10
12
14
16
18
20
0
20
40
60
80
100
120
140
160
180
200
−200
−100
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
Days relative to emigration


Ichiko
E1C
PdG
Estimated
Ovulation
Pregnant
PdG (ug/mg creatinine)
E1C (ng/mg creatinine)
0
2
4
6
8
10
12
14
16
18
20
0
20
40
60
80
100
120
140
160
180
200
0
100
200
300
400
500
600
700
800
900
1000
Days relative to emigration



Y-axes are displayed with an upper limit of 20 ug/mg for PdG and 200 ng/mg for E_1C. X-axes represent the day relative to the date of natal transfer. Blank spaces represent the out of study periods.

Fig 3-2. Hormonal profiles in urinary PdG and E_1C levels for (a) non-conceptive and (b) conceptive ovulatory cycles



Y-axes are displayed with an upper limit of 10 ug/mg for PdG and 100 ng/mg for E_1C. X-axes represent the day relative to the date of estimated ovulation.

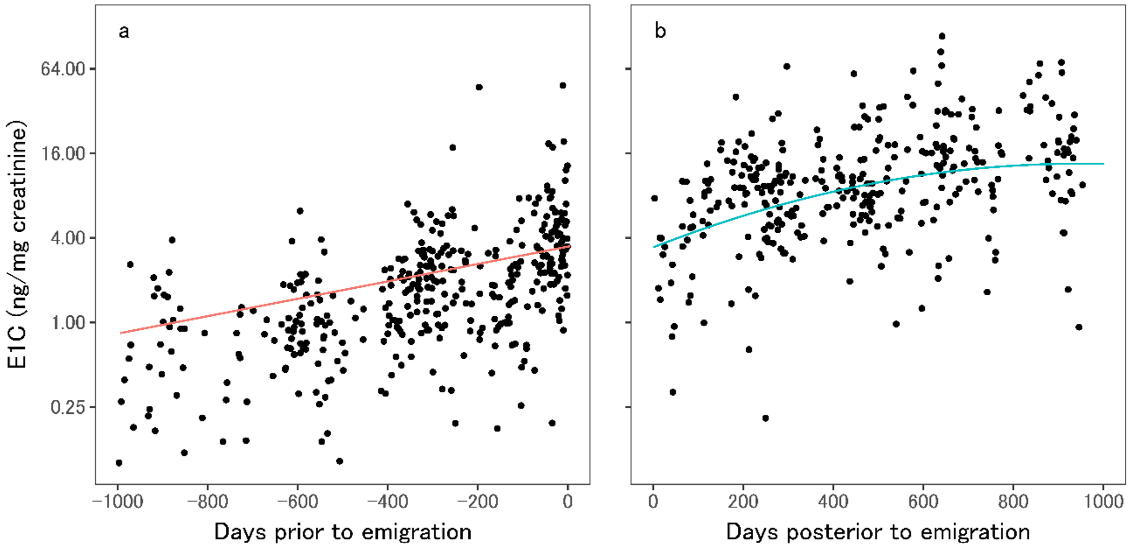
Table 3-3. Outputs of GLMM 1 for urinary E_1C levels

Model	Predictor	Estimate	SE	*t*	*p*
(a) prior to emigration	(Intercept)	0.539	0.139	3.87	0.007
	Day	0.412	0.046	9.04	< 0.001
(b) posterior to emigration	(Intercept)	2.170	0.173	12.56	0.001
	Day	0.430	0.047	9.21	< 0.001
	Day^2	–0.119	0.047	–2.54	0.011

The time relative to the date of natal emigration as a predictor variable is a 3-month interval.

Significant *p*-value is < 0.05.

Fig. 3-3. Changes in urinary E_1C levels prior and posterior to natal emigration



Regression lines were drawn with parameter estimates of the GLMM 1 (a & b) (Table 3-2).

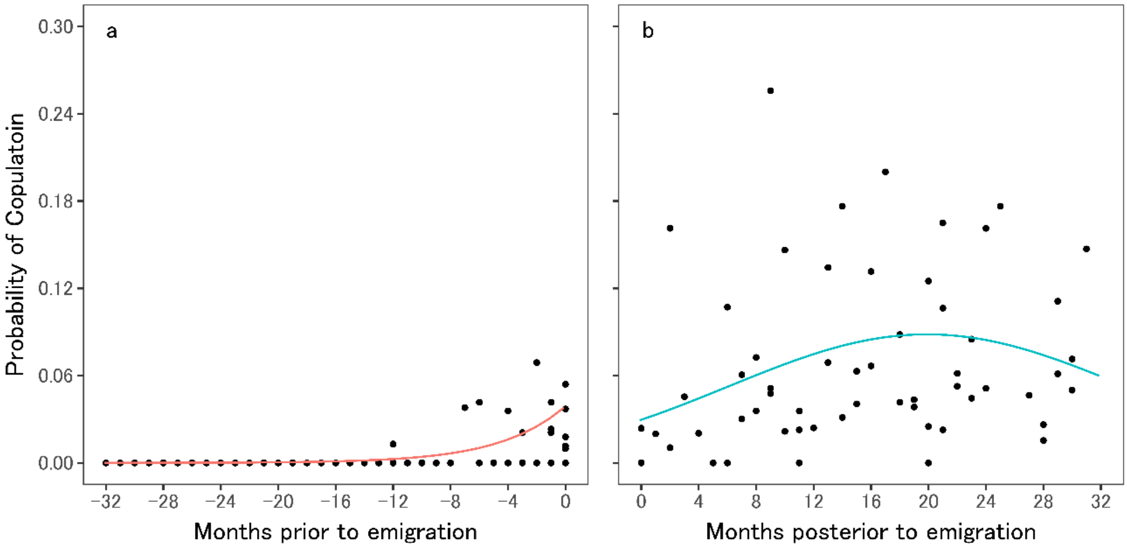
Table 3-4. Outputs of GLMM 2 for copulation rates

Model	Predictor	Estimate	SE	*t*	*p*
(a) prior to emigration	(Intercept)	–6.859	0.703	–9.76	< 0.001
	Time	2.158	0.580	3.72	< 0.001
(b) posterior to emigration	(Intercept)	–2.645	0.132	–33.40	< 0.001
	Time	0.223	0.088	2.53	0.012
	Time^2	–0.236	0.090	–2.64	0.008

The time relative to the date of natal emigration as a predictor variable is a 3-month interval.

Significant *p*-value is < 0.05.

Fig. 3-4. Changes in the probability of copulation prior and posterior to natal emigration



Regression lines were drawn with parameter estimates of the GLMM 2 (a & b) (Table 3-3), respectively.

Chapter 4

Low resistance of older resident females toward female immigration in bonobos (*Pan paniscus*) at Wamba, Democratic Republic of Congo

1. Abstract

Female aggression against outgroup conspecifics is an important aspect of intergroup relationships among female primates. Intense aggression from resident females toward immigrant females suggests that the costs of intrasexual competition outweigh the benefits of group living, and has been reported in some species with female transfer. In bonobos (*Pan paniscus*), however, immigrant females are likely to integrate smoothly into an unfamiliar group through affiliative interactions with specific older females. I hypothesized that older resident females 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 adolescent or adult sons on the probability of aggression by resident females against immigrant females. I collected 73 instances of dyadic agonistic interactions between 14 female bonobos at Wamba, Democratic Republic of Congo, for five different periods between November 2014 and June 2018, which included four immigrant females with a group tenure of less than 2.5 years. The female dominance hierarchy correlated with age and tenure, the slope of the hierarchy was weak but statistically significant and the hierarchy was not linear. 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 findings suggest that the cost imposed by female immigration varies among resident females, and that social tolerance to immigrant females may be associated with low feeding competition rather than any future benefits.

2. Introduction

Dispersal from a familiar group and immigration into another established group (Isbell and Van Vuren 1996), is one of the most important aspects of intergroup relationships. It contributes to gene flow between groups, and its pattern affects the genetic structure of local populations (Eriksson et al. 2006; Forcina et al. 2019). Changes in group size and composition associated with intergroup transfer could affect the reproductive success of individuals within the group (Gillespie and Chapman 2001; Robinson 1988; van Noodwijk and van Schaik 1999). For guenons (*Cercopithecus* spp), female philopatry is the predominant pattern, but female transfer is a common feature in African apes and atelines (Moore 1984; Lee and Strier 2015). Philopatry can be advantageous for females in terms of cooperative defense of limited resources with familiar conspecifics, including kin (Cheney 1992; Wrangham 1980). In species with female transfer, resident females may try to prevent female immigration when the ecological and social costs of intrasexual competition outweigh the benefits of grouping (Sterck et al. 1997; Watt 1991). Understanding the social relationships between resident and immigrant conspecifics may extend our knowledge of primate social structures.

Some level of intense aggression from resident females to new immigrant females settling into the group has been reported in several primate species with female transfer. For example, in chimpanzees (*Pan troglodytes*) and Geoffroy's spider monkeys (*Ateles geoffroyi*), resident females use aggression to repulse new immigrant females from their core areas (Kahlenberg et al. 2008a; Riveros et al. 2017), within which the quality of food resources affects their reproductive rates (Asensio et al. 2015; Thompson et al. 2007). In mountain gorillas (*Gorilla beringei*), resident females may harass new immigrant females (Watts 1991; 1994) due to social competition for access to the silverback for protection of their offspring (Harcourt and Greenberg 2001). Immigrant female northern muriquis (*Brachyteles hypoxanthus*) are displaced from a food patch by resident females at a comparatively high frequency (Printes and Strier 1999). Such conflict between immigrant and resident females may result in disadvantages, such as nutritional sufficiency and social stress, for females in the process of integrating into unfamiliar groups (Printes and Strier 1999; Walker et al. 2018).

In bonobos (*Pan paniscus*), however, immigrant females are unlikely to experience spatial isolation and intensive aggression from resident females (Furuichi 1997; Idani 1991; Sakamaki et al. 2015). Female bonobos typically transfer from their natal group to other groups and remain in the new group after their first parturition (Kano 1992; Sakamaki et al. 2015). In bonobo society, unrelated females in a group aggregate and socialize with one another (Furuichi 2011; Moscovice et al., 2017; Yamamoto 2015). Abundant food resources including large patches of fruit-bearing trees and/or widely available terrestrial herbaceous vegetation may facilitate the high gregariousness of female bonobos (Badrian and Badrian 1984; White and Wrangham 1988). The relatively low necessity of feeding competition may reduce the conflict between resident and immigrant females.

Nonetheless, immigrant female bonobos are usually subordinate to resident females (Furuichi 1997; Sakamaki et al. 2015; Surbeck and Hohmann 2013). Female dominance ranks in bonobos correlate with age and/or group tenure, as in other great apes (Foerster et al. 2016; Robbins et al. 2005). Older female bonobos are dominant over most males and play a central social role in the group (Furuichi 1989; Parish 1996; Tokuyama and Furuichi 2016; 2017). Further, immigrant females may allocate more time and effort to establishing affiliative relationships with one specific older female than other resident females (Idani 1991). Affinity with older resident females occupying high dominance ranks might be important for immigrant females to access the central part of the new group for feeding and socializing (Idani 1991). However, it remains unclear whether older resident females are more tolerant of unfamiliar young females than younger resident females?

In bonobos, mothers have a strong influence on the reproductive success of their sons (Surbeck et al. 2019). Mothers can provide agonistic aid to their sons in male-male competition (Furuichi 1997; Surbeck et al. 2011) and maternal rank may correlate with the son's rank (Furuichi 1997; Ishizuka et al. 2018). Further, female immigration is beneficial for resident males due to the increased number of future reproductive partners (Kahlenberg et al. 2008b; Watts 1991). Resident females may also gain indirect reproductive advantages from immigrant females through their philopatric sons. I hypothesized that older female bonobos with mature sons are tolerant toward immigrant females due to a future benefit. If this is the case, older resident females and those with mature sons should be less aggressive to immigrant females than younger resident females and those without mature sons. I therefore examined the effect of (1) age and tenure and (2) the presence of adolescent or adult sons on the rate of aggression by resident females against immigrant females.

3. Methods

3-1. Study site and group

KT conducted field observations at a long-term field site for bonobo research at Wamba, in the northern sector of Luo Scientific Reserve, Democratic Republic of Congo (Kano 1992; Furuichi et al. 2012). Since 1974, researchers have conducted behavioral observations of wild bonobos using provisioning. The bonobos in one main study group, called "E1", were all individually identified by 1986 (Furuichi 1989; Kano 1992). Field research was interrupted owing to a civil war between 1996 and 2002. However, continuous observations of the E1 group resumed without artificial provisioning in 2003. Researchers completed the re-identification of all bonobos in the E1 group in 2006 (Hashimoto et al. 2008). The E1 group ranges over primary, old and young secondary forest, swamp, and agricultural field (Hashimoto et al. 1988; Terada et al. 2015).

3-2. Study subjects

The E1 group consisted of 31 to 43 individuals, including 8 to 9 adult males (15 years and older; Hashimoto 1997), 3 to 5 adolescent males (8 to < 15 years old), 9 to 12 adult females (parous, or 15 years or more), and 2 to 5 adolescent females (nulliparous, and 8 to < 15 years old). All these females had immigrated to the E1 group from other groups, and researchers estimated their year of birth based on their physical features (Table 4-1; see also Sakamaki et al. 2015). I considered adolescent and adult male offspring of the females as mature sons, as previous studies have shown that male bonobos start to reproduce at 7 years of age (Thompson-Handler 1990).

Females from other groups are often considered as immigrants until their first reproduction occurs, after which they are considered as residents (Kehalenberg et al. 2008a; Riveros et al. 2017). The median interval between immigration and first reproduction was reported as 2.5 years in female bonobos at Wamba (Sakamaki et al. 2015), and thus I classified female bonobos as immigrants if they had spent less than 2.5 years in a group, and residents after 2.5 years. The four immigrant females in this study (Pf, Ik, Sc, and Db) were well habituated at the beginning of the study because they came from adjacent study groups to the west of the E1 group, called “PE” and “PW” groups where individual identification has been conducted since 2010 (Sakamaki et al. 2018).

3-3. Data collection

I observed E1 group for 2406 hours during five periods: (1) November 2014 to February 2015, (2) July to October 2015, (3) May to October 2016, (4) February to July 2017, and (5) February to June 2018. I followed bonobos from before they moved out of their night nests (usually around 06:00) until they made new night nests (usually around 17:00; Mulavwa et al. 2010). Bonobos exhibit fission-fusion social dynamics where membership of a group is flexible and changes fluidly (Kuroda 1979; White 1988). I defined a party using the one-hour party method proposed by Hashimoto et al. (2001), determining party membership and size as all the individuals observed within a one-hour segment (e.g., 6:00 to 7:00, 7:00 to 8:00, and so on). I recorded the individuals present from the beginning to the end of each one-hour segment. The 2,278 one-hour party segments included a mean of 6.9 ± 2.9 SD females.

KT recorded all observable agonistic interactions between females, including both contact aggression and directed displays (de Waal 1988; Furuichi 1997). I defined contact aggression as any physical attack, such as beating, pushing, pulling, kicking, and biting. I defined a directed display as charging, chasing, and branch dragging. When coalitionary aggression occurred, with two or more females chasing one common target (Harcourt and de Waal 1992; Tokuyama and Furuichi 2016), I distinguished the first actor from the accompanying actors and counted the event as an agonistic interaction between the first actor and her target, because of the difficulty in evaluating a power relationship between the accompanying actors and the target.

3-4. Data analysis

I observed 73 dyadic agonistic interactions in 91 female-female dyads (please see Supplementary Table S4-2). To establish a dominance hierarchy, I calculated David's scores (David 1987) for each female ($N = 14$) based on dyadic dominance indices, in which the proportion of wins and losses were corrected for the chance occurrence of these interactions (de Vries 1998). I used a Spearman's rank correlation to examine the relationships between age and tenure and David's score. I converted David's scores into normalized David's scores, that varied between 0 and $N–1$ (de Vries et al. 2006). Regressing the NDS ranks against the NDS values provides the steepness of the hierarchy, which varies between 0 and 1. I assessed the significance of this steepness through 10,000 randomizations of the observed matrix, using the "steeptest" function in the "steepness" package (de Vries et al. 2006) in R software (version 3.6.1, R Core Team 2019). I also calculated the h' index (de Vries 1995) as a modified version of Landau's linearity index (Landau 1951) to determine whether the female dominance hierarchy is linear or not. I compared the h' index was with the expected h' value generated in the 10,000 randomizations.

To examine the effect of age, tenure, and presence of mature sons of resident females on the probability of aggression against immigrant females, I used a generalized linear mixed model (GLMM) with a Poisson error structure and a log link function (Zuur 2009), using the "glmer" function of the "lme4" package in R (Bates et al. 2015). The response variable was the number of agonistic behaviors made by 10 resident females against four immigrant females (i.e., 40 resident-immigrant dyads). When immigrant females became resident females (i.e., when they had been in the group for >2.5 years), I excluded them from analysis to standardize the number of resident females for each immigrant female. I controlled for differences in observation times between the 40 dyads by including the number of one-hour segments in which I observed each dyad together as an offset term in the model. The explanatory variables were the age (16 to 47 y) and tenure (6 to 34 y) of resident females, and the presence vs. absence of mature sons. Before running the model, I standardized the covariates age and tenure to a mean of zero and a standard deviation of one. I included immigrant's ID and resident's ID as a random variable to account for pseudo-replication.

To check the assumption of the full model, I calculated variance inflation factors (VIF, Quinn and Keough 2002), using the "vif" function in the "car" package (Fox and Weisberg 2018). The VIF values of the explanatory variables of the age, tenure, and presence of mature sons were 15.7, 13.8, and 1.65, respectively, and thus collinearity between age and tenure was a considerable issue (Zuur et al. 2010). I reran two GLMMs which considered the explanatory variables of the age and tenure, separately, in addition to son presence. The age model (AIC = 73.64) was slightly better than the tenure model (AIC = 75.35), so I interpreted the results of the age model. Collinearity was not an issue in the age model (largest VIF = 1.44). I tested the model with a Poisson error structure for overdispersion (Faraway 2006), which was not an issue (dispersion parameter = 1.08, $\chi^2 = 37.8$, $df = 35$, $P = 0.342$). Finally, I compared the age model and null model that only consisted of the random variables using the "anova" function in R (Dobson and Bernett 2008).

4. Results

Most female aggression was by older females against younger females (67 of 73 instances). Females' David's scores based on dyadic dominance indices were significantly correlated with their age ($N = 14$, $r_s = 0.931$, $P < 0.001$) and tenure ($N = 14$, $r_s = 0.925$, $P < 0.001$). The slope of the linear regression of the ranks against the normalized David's scores was $R^2 = –0.153$ (Fig. 4-1). This observed steepness was significantly greater than a randomly generated steepness (one-tailed $P < 0.001$). The linearity index h' of 0.276 was not significantly different from the expected h' value of 0.200 (one-tailed $P = 0.257$).

I observed 17 instances of aggression initiated by resident females against immigrant females, which occurred in 12 of the 40 resident-immigrant dyads. The full model, testing the effects of the age of resident females and the presence of mature sons on the probability of aggression, while controlling for the number of the one-hour segments in which each dyad was observed together, was significantly different from the null model ($\chi^2 = 8.28$, $df = 2$, $P = 0.020$). Age had a significant negative effect on the probability of aggression, but the effect of the presence of mature sons was non-significant (Fig. 4-2; Table 4-2). This GLMM result indicates that older resident females were less aggressive against immigrant females than relatively younger resident females and that the presence of mature sons was not significantly related to female aggression against immigrant females.

5. Discussion

I found that older resident female bonobos were less aggressive toward immigrant females than younger resident females were. In contrast to the prediction, however, resident females with mature sons did not differ from those without mature sons in the rate of aggression against immigrant females. My results do not support the hypothesis that older female bonobos tolerate female immigration to receive an indirect benefit through their philopatric sons. This study implies that the high tolerance of older resident females is not necessarily associated with the potential future reproductive advantage they accrue if their sons breed with the new females.

Older resident female bonobos occupied higher ranks than young immigrant females, who were positioned at the bottom of dominance hierarchy. The female dominance hierarchy I observed was significantly but weakly steep but not significantly linear. My results are consistent with previous studies of bonobos (Furuichi 1997; Sakamaki et al. 2015; Surbeck and Hohmann 2013; Stevens et al. 2007). Similar age-related female-female agonistic relationships are seen in chimpanzees (Foerster et al. 2016) and mountain gorillas (Robbins et al. 2005), but evidence for agonistic dominance hierarchy is weak in female western lowland gorillas (*Gorilla gorilla*: Stokes et al. 2004). The rarity of aggressive challenges to older dominant females appears to be common among female African great apes, and contrasts with the pattern found in many primate species with female philopatry. In many cercopithecines, for example, daughters inherit their mother’s rank (Berman 2017). In other cases, female dominance ranks gradually decline with age after sexual maturation (e.g., hanuman langurs, *Semnopithecus entellus*: Borries et al. 1991).

Nonetheless, agonistic relationships of resident females toward immigrant females considerably differs between the *Pan* species. This study indicates that older resident females have a lower rate of aggression against immigrant females than younger resident females. The pattern is not known in other species with female transfer. Female chimpanzees living in higher-quality core areas are more aggressive toward immigrant females than other resident females are (Kahlenberg et al. 2008a), suggesting that aggression against newcomers might be associated with the quality of core areas. Immigrant female chimpanzees also tend to be subordinate to natal adolescent females of a similar age (Kahlenberg et al. 2008a). Maternal presence appears to help non-dispersing daughters in their initial rank acquisition, which can be subsequently more advantageous for their reproduction in chimpanzees than immigrant females (Foerster et al. 2016; Walker et al. 2018). The study group did not include natal females (non-dispersing females) for comparison with these findings for chimpanzees.

The hostility of resident females to immigrant females may depend on the immediate costs imposed by female immigration, such as feeding competition (e.g., Kahlenberg et al. 2008a; Printes and Strier 1999; Riveros et al. 2017). Although female bonobos aggregate with each other, higher-ranking females tend to occupy a better place to access food resources (i.e., intake rate per minute, probability of interpatch movement) than lower-ranking females (Nurmi et al. 2018). Given the age-related female dominance hierarchy, younger females may face a higher cost led by female immigration than older females do. Aggression can be exchanged or escalated more often among closer-ranking females than those that are very different in rank (e.g., Barrett et al. 2002; Vogel et al. 2007), as individuals generally avoid fighting with clearly dominant opponents (Parker 1974). My results suggest that younger resident females might need to use aggression to dominate younger immigrant females in the same patch, whereas older resident females may not need to do so.

In Lui Kotale bonobos, agonistic interactions are seen more often among female dyads with relatively shorter co-residence in the same group than between longer-term co-residents (Moscovice et al. 2017). My results partially match the previous finding in that aggression occurred more often between resident and immigrant females than among older resident females with similar tenure. As female dominance ranks become established in the group, the rate of female aggression may decrease. The tendency also applies to other species with female transfer. For example, in Geoffroy's spider monkeys, the rate of female aggression against immigrant females decreases sharply 6 months after they arrive in the new group (Riveros et al. 2017). In northern muriquis, immigrant females were often targeted only during the season in which they joined the group (Printes and Strier 1999). Established dominance relationships may reduce agonistic interactions for access to food resources (Parker 1974). Further studies examining patterns of female-female agonistic interactions based on social dynamics are required to extend our knowledge about generational relationships in species with female transfer.

I provide an example of tolerance in resident females, particularly older females, toward immigrant females in bonobos. Immigrant females might benefit from the tolerance and dominance of older resident females (Idani 1991), who play a central role in the group (Tokuyama and Furuichi 2017; Parish 1996), such as their readiness to permit co-feeding in a given food patch (Parish 1994; Yamamoto 2015) and the availability of coalitionary defense against male harassment (Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016). However, given the small sample size of immigrant females and limited social dynamics in this study, caution should be taken when drawing conclusions from my results. For example, nulliparous female bonobos tend to make repeated visits to other groups, for temporary periods ranging from a few days to several months (Kano, 1992; Sakamaki et al. 2015). However, no such temporary visitors appeared in E1 group during this study. Conflict and affinity with resident females may be one of the factors affecting whether immigrant females remain in a new group or leave.

Abundant food resources facilitate intergroup associations with less female aggression (Kinnarid 1992; Sakamaki et al. 2018). Females may benefit from affiliative intergroup relationships, such as intensified defense against predators or sharing valuable food resources without risk of injuries (Grueter et al. 2012; Pisor and Surbeck 2019). So far, however, the benefit of tolerance of immigrant females for resident females has been not examined in species with female transfer. The increase in females in the group as mating partners for philopatric males is a conceivable potential benefit for their mothers. However, I did not find that female aggression against immigrant females was affected by the presence of mature sons in bonobos, perhaps because such a future benefit is too uncertain.

In summary, I showed that the rate of female aggression against immigrant females decreased with age in resident females, but was unrelated to the presence of mature sons in bonobos. My findings suggest that the costs of intrasexual competition imposed by female immigration on resident females vary within the group and between species. Further studies of social interactions between resident and immigrant females are required in primates with female transfer, to better understand the socio-ecological factors enhancing social tolerance among female primates.

Table 4-1. Profile of female subjects in E1 group of bonobos at Wamba, DRC, in June 2018

ID	Estimated year of birth[a]	Estimated age (years)[b]	Month & Year of immigration	Tenure in E1 group (years)	ID (birth year) of mature son(s)
Resident					
No	1971	47	Nov.1983	34	
Ki	1974	44	Dec.1984	33	NB (1988); KT (2004)
Hs	1981–85	35	Feb.1996–Aug.2003[d]	18	
Sl	1991–92	27	Feb. 1996–Aug. 2003[d]	18	SB (2004)
Yk	1981–85	35	Apr.2004[e]	14	
Jk	1986–90	30	Apr.2004[e]	14	JR (2001); JO (2006)
Nv	1994–95	23	Aug.2007	11	
Fk	1998	20	Apr.2008	10	
Ot	1997	21	Jun.2008	10	
Zn	2002	16	Oct.2011	6	
Immigrant					
Pf	2003–05	14	Oct.2013	4	
Ik	2007–08	10	Oct.2014	3	
Sc	2008–09	9	Nov.2015	2	
Db	2009	9	Aug.2016	1	

[a] I estimated year of birth based on physical features and reproductive profiles (Sakamaki et al. 2015).

[b] I calculated age was from the midpoint of the estimated birth year.

[c] Hs and Sl were identified after research resumed in 2003 (Hashimoto et al. 2008).

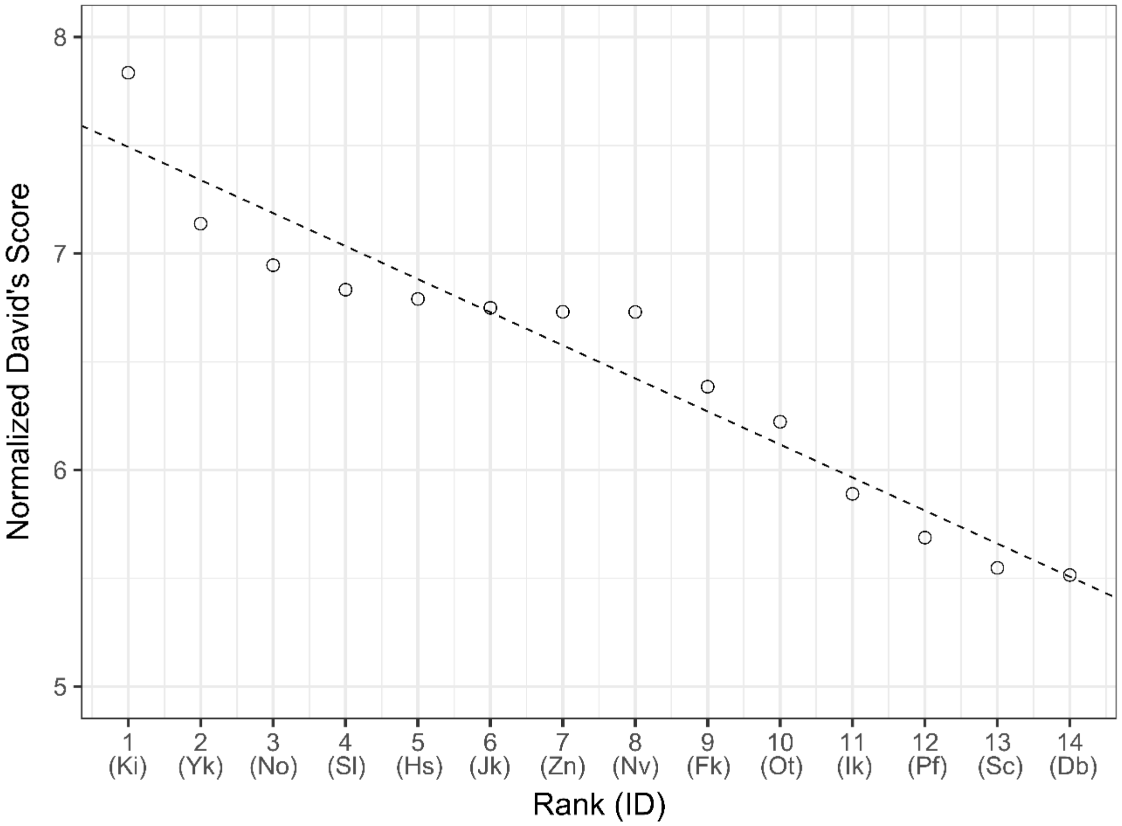
[d] Yk and Jk and their infants were identified after research resumed in 2003. They were assumed

to come from adjacent groups that disappeared while research was interrupted (Hashimoto et al. 2008).

Table S4-2. Matrix of dyadic agonistic interactions among 14 female bonobos

	No	Ki	Hs	Yk	Jk	Sl	Nv	Ot	Fk	Zn	Pf	Ik	Sc	Db	*Win*
No	*	0	0	0	3	2	0	0	0	0	0	0	0	0	5
Ki	0	*	2	1	6	3	1	0	1	0	1	0	0	0	15
Hs	0	0	*	0	0	3	0	0	0	0	0	1	1	1	6
Yk	0	0	0	*	0	0	1	2	0	1	1	0	1	0	6
Jk	0	0	0	0	*	1	0	0	0	1	0	0	0	0	2
Sl	0	0	0	0	0	*	0	1	1	2	3	3	1	0	11
Nv	0	0	0	0	0	0	*	1	1	0	0	0	0	1	3
Ot	0	0	0	0	0	0	0	*	0	1	0	2	0	1	4
Fk	0	0	1	0	0	0	0	0	*	0	1	0	0	1	3
Zn	0	0	0	0	0	1	0	2	1	*	3	2	0	0	9
Pf	0	0	0	0	0	0	0	0	0	0	*	0	2	1	3
Ik	0	0	0	0	0	0	0	0	0	0	1	*	2	0	3
Sc	0	0	0	0	0	0	0	0	0	0	0	0	*	2	2
Db	0	0	0	0	0	0	0	0	0	0	0	0	1	*	1
Lose	0	0	3	1	9	10	2	6	4	5	10	8	8	7	73

Fig. 4-1. Normalized David's scores plotted against the rank of 14 female bonobos, Ki–Db, ranked from 1 (highest) to 14 (lowest)



Data are for bonobos at Wamba, DRC, between November 2014 and June 2018. I fitted the regression line from the normalized David's scores; with a slope of –0.153 and an intercept of 7.645.

Fig. 4-2. Probability of aggression by 10 resident females against 4 immigrant females (rate of aggression per time the females were observed together)

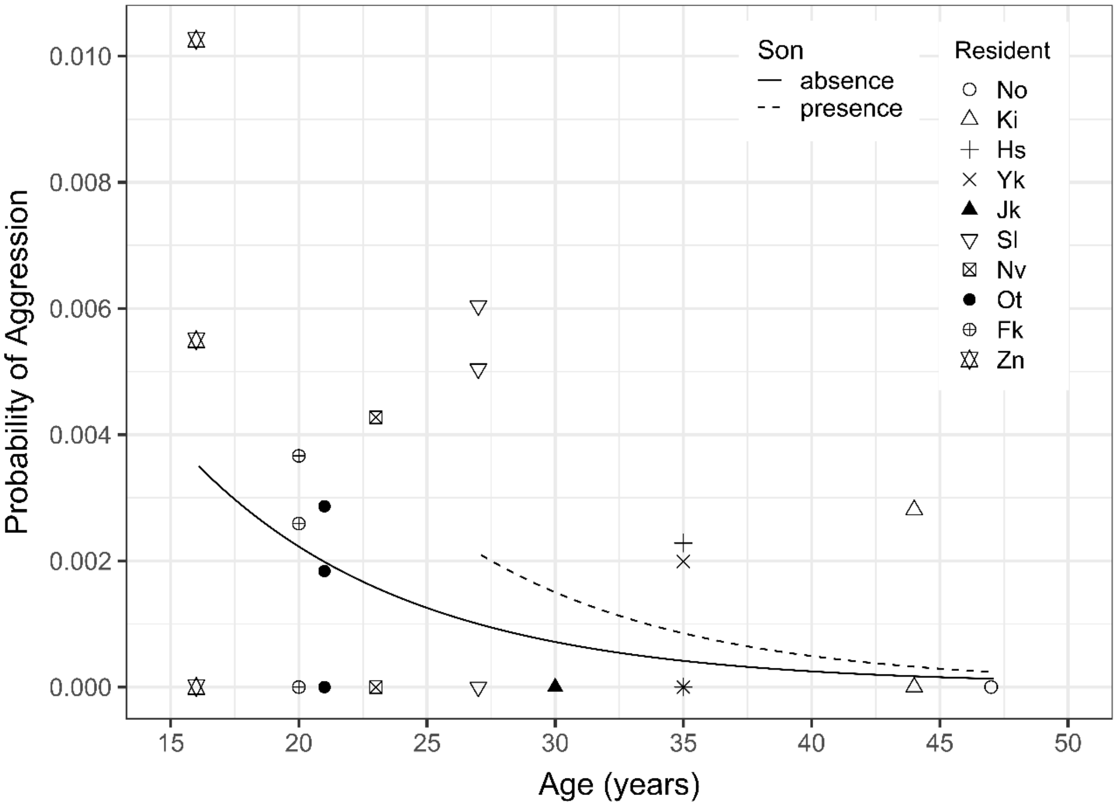


Table 4-3. The effects of age and presence of a mature son on the probability of aggression by resident females against immigrant females in bonobos

Predictor	**Estimate**	**SE**	***Z***	***P***
Intercept	-7.419	0.483	-15.37	< 0.001
Age	-1.057	0.410	-2.58	0.010
Son presence (0 = No; 1 = Yes)	0.774	0.606	1.28	0.202

Chapter 5: General Discussion

1. Summary of results

In Chapter 2, I reported a difference between male and female bonobos in that the females decreased party associations with their mothers prior to natal emigration (6.78 ± 0.25 years old) while the males kept relatively high associations with their mothers through the juvenile period. This difference emerged at six to seven years of age in juvenile bonobos, and female bonobos achieved dissociation from their mothers at an earlier age than did male bonobos. As hypothesized in some previous studies (Cords et al. 2010; Fairbank 1993; Nicolei and Borries 1997), my findings in juvenile bonobos may be based on the social characteristics of adult bonobos where mothers are important supporters of their sons' mating rates, and unrelated females are cooperative with each other. By contrast, in the sister species, male chimpanzees begin dissociating from their mothers at an earlier age than do females (Hayaki 1988; Pusey 1983; 1990). This contrast between the close species emerging during the juvenile period implies that offspring-mother relationships can vary depending on the social relationships and reproductive strategies of each sex in adult social lives.

In Chapter 3, I suggested that female bonobos may emigrate at the early stage of puberty. Urinary E_1C and copulation rates increased prior to emigration and reached an upper maximum thereafter. However, I did not find any ovulatory signals implied by a sustained rise of urinary PdG until at least one year after emigration. My findings are in line with observational knowledge that female bonobos exhibit undeveloped sexual swelling and behaviors like adult females (Hashimoto 1997; Sakamaki et al. 2015). These results imply that the onset of ovarian development stimulated by gonadotropins and the activation of sexual behaviors can be criteria for natal emigration in female bonobos. The prolonged period between emigration and sexual maturation can be hypothesized as a function to avoid the energetic costs of first reproduction until they are established in the new group (Strier and Ziegler 2000) or to allocate more time to choose better groups before they become fertile.

In Chapter 4, I showed that female bonobos form a weak, non-linear dominance hierarchy correlating with age and that older resident females were less aggressive toward new immigrant females than relatively younger resident females irrespective of the presence of mature sons. This result implies that the high tolerance of older resident females is not necessarily associated with the potential future reproductive advantage they accrue if their sons breed with the new females. Although this age-ordered dominance hierarchy is also seen in female chimpanzees (Foerster et al. 2016), their rank-ordered pattern of aggression against newcomers appears to be contrary to female bonobos. Kahlenberg et al. (2008b) report that higher-ranking female chimpanzees occupying better core areas are more aggressive than lower ranking females toward immigrant females. Bonobos might have a generational structure that reduces the conflict between young immigrant females and old resident females.

2. Proximate causes of female transfer

Natal dispersal can be a selective advantage as part of a life-history strategy on an evolutionary timescale when the fitness benefits of migration from an original group to a new group exceed the fitness costs (Bowler and Benton 2005). Physical growth and social development may be fixed as the basic thresholds at natal dispersal because younger individuals are more vulnerable (Alberts and Altmann 1995; Janson and van Schaik 1993; Nicolson 1987; Pereira 1988). However, even if they pass the thresholds, decisions to emigrate from the natal group can depend on body conditions and socio-ecological environments, as is the case for non-dispersing parous females (Moscovice et al. 2017; Nakamura 2015; Robbins et al. 2009; Walker et al. 2018).

The weakened social relationships with mothers are one of the major changes preceding dispersal (Colvin 1986). Indeed, I found a decline in party associations with mothers in female bonobos at six to seven years prior to natal emigration (Chapter 2). The onset of dissociation from mothers appears to be earlier in female bonobos than in female chimpanzees, corresponding to their difference in age at natal emigration. In addition, Lee et al. (2019) have shown that weaning, i.e., ceasing to suckle the mother's nipple and ride on the mother's back, comes at a similar age, but spatial security with a distance from mothers may be at different levels between the *Pan* species. Mother chimpanzees may be sensitive to the threat of male aggression toward their infants (Otali and Gilchrist 2006). Although male bonobos can also be aggressive toward juveniles, this aggression has never been shown to be lethal (Gottfried et al. 2019). Further, the presence of mother chimpanzees may be beneficial to independent daughters in that they can share core areas and cooperate with each other (Foerster et al. 2016; Kahlenberg et al. 2008b). In bonobos, although mothers often share valuable food resources with juvenile daughters, this food sharing can also occur between unrelated females (Jaeggi et al. 2010; Yamamoto 2015). Differences in the relative benefits of maternal presence compared to other individuals for daughters might reflect the age of natal emigration for each *Pan* species.

Since the risk of inbreeding occurs with the onset of ovulation, natal emigration is expected to correlate with hormonal and behavioral changes of puberty. In Chapter 3, I reported that urinary E_1C levels increased prior to emigration in female bonobos but PdG-defined ovulation was not detected until at least one year after the emigration; thereby, natal emigration may occur at the early stage of puberty. Female bonobos were observed to perform a few copulatory interactions with mature males of their natal group before emigration, but the probability of fertilization with these copulations is negligible. Then, female bonobos prior to emigration became more active in engaging in copulations than those posterior to emigration. My results do not contradict the expectation of the "inbreeding avoidance" hypothesis, although the effects of hormonal activation (e.g., Holekamp and Smale 1998; Nunes et al. 1999) or outbreeding motivation (e.g., Corely et al. 2017; Lehmann and Perrin 2003; Walker and Pusey 2020) on natal emigration are unknown. Nonetheless, I should note that the stage of sexual development at female transfer can be determined strategically for each species and does not exist fixedly for all species (Crockett and Pope 1993; Kahlenberg et al. 2008a; Robbins et al. 2009; Strier and Ziegler 2000; Shimooka et al. 2008; Stumpf et al. 2009).

Further, encounter with neighboring groups are important opportunities for immigration into another group (Sicotte 1993; Strier et al. 2015; Struhasker, 2010) without the costs of solitary intergroup movement (Isbell and van Vuren 1996). As described in previous bonobo studies at Wamba (Furuichi 1989; Idani 1990; Kano 1992; Sakamaki et al. 2015), almost all subject females in my research transferred out of their natal group through intergroup encounters. Although intergroup encounters coincide with the season of fruit abundance, which is a factor in facilitating intergroup tolerance (Lucchesi et al. 2020; Sakamaki et al. 2018), female transfer can be conducted irrespective of fruit abundance when intergroup encounters occur (Toda et al. unpublished data). This study suggests that several developmental thresholds may exist behind natal emigration, but encounters with members of other groups is likely to be a critical trigger driving female transfer.

3. Socio-ecological characteristics determining dispersal costs

Costs are ubiquitous at different phases of the dispersal process and vary considerably depending on the socioecological characteristics of a species (Bonte et al. 2012; Isbell and van Vuren 1996). Resident individuals' social behavior toward outgroup conspecifics may be one of the factors driving variation in social dispersal. For example, emigrant female red howlers (*Alouatta seniculus*) can suffer severe aggression from resident females, and thus, they try to form a new group rather than immigrate into an established group (Crockett and Pope 1988; 1993). On the other hand, female western red colobuses (*Pilicolobus badius*) move flexibly between groups without suffering harassment from resident females (Struhsaker 2010).

As discussed in Chapter 2, the high social tolerance of female bonobos toward unfamiliar females can relieve the costs of immigration into an established group. In Wamba bonobos, although immigrant females are positioned at lower ranks than resident females in the group, resident females are less hostile to immigrant females and aggregate with each other (Furuichi 1989; Idani 1991; Sakamaki et al. 2015; Surbeck and Hohmann 2013; Chapter 4), and thus, immigrant females are unlikely to be vulnerable to aggression by resident females or to predation due to social isolation. Further, in supplementary data (Toda unpublished data), I found that close-to-emigration females (CEFs) and recently immigrant females (RIFs) received aggression from resident females with a similar rate (Fig. S5-1a). On the other hand, RIFs were more often targeted than CEFs by resident males (Fig S5-1b). Nonetheless, male aggression against immigrant females is often not severe and sometimes changes to a playful interaction (Sakamaki et al. 2015; Gottfried et al. 2019). In addition, older females occasionally provide younger females with cooperative aggression against male harassment (Tokuyama and Furuichi 2016). Thus, the social stress associated with female transfer can be comparatively low in bonobos.

By contrast, in chimpanzee society, a large gap in female social life between the natal group and the new group is likely to exist because resident females can be hostile toward immigrant females over food resources (Boesch and Boesch-Ackermann 2000; Kahlenberg et al. 2008b; Nishida 1989; Pusey 1990). Female chimpanzees have long-lasting social bonds with a few specific females, including kin, rather than cooperating indiscriminately with many females (Foerster et al. 2015; Langergraber et al. 2009; Lehmann and Boesch 2009). Thus, mothers in the natal group may be more important partners than other adult females for the association and interaction of female chimpanzees. Some female chimpanzees may choose to remain in their natal group to take advantage of inheriting maternal core areas and ensuring initial rank (Foerster et al. 2016; Kahlenberg et al. 2008b). Walker et al. (2018) report that immigrant females experience a three-year delay in first reproduction compared to philopatric females, which might indicate the depressive effects of energetic loss and social stress associated with female transfer. Further, immigrant females might need to present the “sexual swelling passport” to be accepted by males of the new group (Kahlenberg et al. 2008a; Nishida 1979; Wallis 1992), which could be the threshold at female transfer in chimpanzees.

4. Conceivable functions of early dispersal in female bonobos

Even when bonobo society has relieved the potential costs associated with female transfer, early emigration relative to sexual maturation should have evolved with some fitness benefits, as long as younger females have a larger risk of mortality. As discussed in Chapter 3, one conceivable benefit of early emigration is postponing the energetic costs of gestation and lactation until immigrant females become familiar with the established group (Bronson and Rissman 1986; Strier and Ziegler 2000). This strategy can be expected to play a role in smoothing the beginning of their reproductive careers once they are mature. However, since nulliparous female bonobos tend to repeat temporary visits among groups through intergroup encounters until they settle down in a specific group (Kano 1992; Sakamaki et al. 2015), this dispersing behavior does not appear to match the above explanation. I propose another dispersal strategy that female bonobos allocate the prolonged period between emigration and sexual maturation to seek better groups based on food availability and male quality. Unlike female Thomas langurs and western red colobus females that secondarily transfer between groups depending on socio-ecological dynamics, female bonobos generally remain in the reproductive groups for life (Hashimoto et al. 2008; Sakamaki et al. 2015), probably because they may need a long time to take care of their offspring or to avoid the degradation of their social status in a new group (Furuichi 1997; Surbeck et al. 2011; Chapter 4). Thus, the female group choice once before first reproduction can be related to their future reproductive success, although it is unknown whether the female reproductive rate varies among bonobo groups.

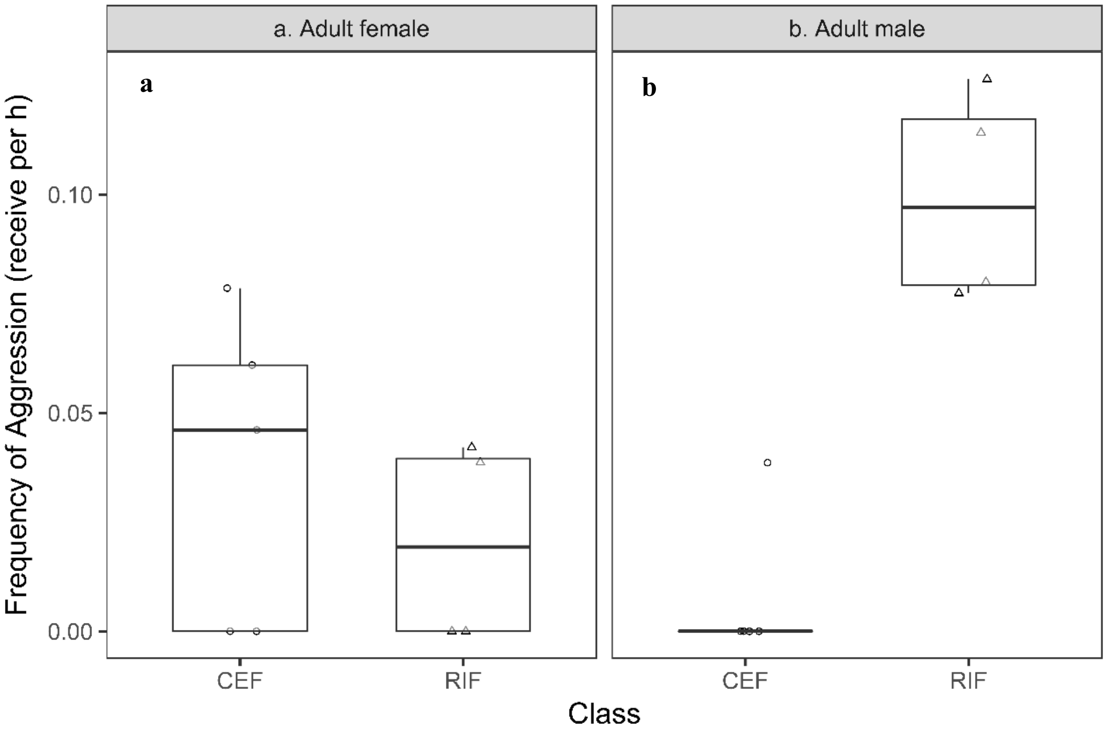
5. Conclusion and future perspectives

In summary, this study revealed that natal emigration of female bonobos may follow the weakened spatial relationships with their mothers (Chapter 2), increasing levels of urinary E_1C levels, and the onset of copulatory interactions with mature males (Chapter 3). In addition, this study reported that older resident females occupying higher ranks were unlikely to be aggressive toward recently immigrant females at the bottom of the dominance hierarchy (Chapter 4). The low developmental threshold of their emigration may be realized by high female tolerance toward immigrant females, and early emigration relative to sexual maturation may be selected strategically for future reproductive life.

For the future progress of this study, I need to focus on the detailed social interactions of female bonobos with mothers and other individuals for a better understanding of their social priority during the process of female transfer, which is hypothesized to be based on current and future benefits (Fairbanks 1993; Kummer 1978). Their partner preference and mate choice might be involved with the proximate mechanisms behind the decisions at different dispersal phases. It also would be interesting to examine the strategies female bonobos take to smoothly integrate into the new group. Further, measuring feeding efficiency and energetic balance along the dispersal phases is important to evaluate substantial dispersal costs (Maag et al. 2019) and examine their counterstrategies. For example, close-to-emigration females may increase their time of spent resting or feeding to conserve energy prior to dispersal (Printes and Strier 1999; Stumpf et al. 2009). Moreover, female bonobos can transfer out of their natal group during the juvenile period before nutritional requirements are increased for first reproduction (Bronson and Rissman 1986; Strier and Ziegler 2000). Furthermore, little is known about hormonal mechanisms for an extended period of sexual swelling in nulliparous females in bonobos (Furuichi 1987; Ryu et al. 2015) and chimpanzees (Wallis 1997; Deschner and Boesch 2007). Exaggerated morphological and behavioral cues of sexual state or fertility are referred to as “adolescent exaggeration,” which have been reported in a large number of primate species, including humans (overview in Anderson and Bielert 1994). In the *Pan* species, female sexual swelling functions to promote associations and interactions with other individuals (Kahlenberg et al. 2008b; Ryu et al. 2015), and thus the prolonged swelling of immigrant females might play a role in attracting resident conspecifics for a smooth social integration into the established group.

Comparative studies on female sociality across different environments are required to generalize female dispersing strategies due to socio-ecological factors. Most studies of wild bonobos, including my study, have been conducted in dense forest habitats where food availability is relatively high and stable (Mulavwa et al. 2008; Nurmi et al. 2018; White and Wrangham 1988), although bonobos inhabit diverse environments, including the mosaic forest which contains both forest and savanna vegetation (Narat et al. 2015; Serckx et al. 2014). Further, more extensive sampling on nulliparous females from different dispersal phases in the genus *Ateles*, *Brachyteles*, *Lagothrix*, *Orenox*, and *Piliocolobus*, as well as the genus *Pan*, would be required to examine how female-biased dispersal (or male philopatry) has been evolutionally selected in primate social systems (Furuichi et al. 2015).

Fig S5-1. Comparisons of the frequency of receiving aggression from (a) adult females and (b) adult males between CEFs and RIFs



CEFs are defined as female bonobos within one year prior to emigration, and RIFs are defined as those within one-year posterior to immigration. I collected behavioral records of five CEFs and four RIFs during 201.4 hours of focal following (one focal session was continued for 30 min). CEFs and RIFs received aggression from resident females at a similar rate (Mann-Whitney U-test: $W = 14$; $p = 0.371$). RIFs received aggression more often than CIFs from resident males ($W = 0$, $p = 0.015$).

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