Female gregariousness and social bonding in the male-philopatric society of bonobos (*Pan paniscus*)

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Abstract

The aim of my research was to study how female gregariousness and affiliative bonding evolved in the male-philopatric society of bonobos. Exploring the mechanism of their social bonding might give us cues for understanding the social bonding in unrelated female animals, including humans. The following studies were conducted by observing wild bonobos in the Luo Scientific Reserve, Democratic Republic of the Congo.

First, I report a case study in which most group members joined to form a large mixed-sex party and travelled a long distance to return to the location of a snare to search for a male group member that had been caught in it and was left behind the previous day. This demonstrates that both females and males have a strong motivation to maintain group cohesiveness in bonobos. Second, I investigated coalition formation behavior among females, that might be related to female gregariousness. The results suggested that female coalitions in bonobos might have evolved as a counter-strategy against harassment by males. There was a uni-directional relationship in which older females agonistically support younger females. Females did not choose their coalition partners based on their affiliative relationships, though staying in the same party was an important factor. Coalitions might enhance gregariousness among females, leading them to develop affiliative interactions that promote tolerance. Since staying with old females may be beneficial for younger females because of the agonistic support received, female cohesiveness may be maintained by the motivation of younger females to follow older ones. To confirm this hypothesis, I examined the leadership patterns of bonobos by observing their group movement coordination. As predicted, old and dominant females were initiators of departures more frequently than other age / sex categories.

This study revealed that strong female social bonding in bonobos might have evolved because being gregarious was beneficial for females to counter harassment from males. Younger females might aggregate around older females to receive agonistic support, and it might be beneficial for older females by providing mating opportunities to their male offspring who usually range with their mother. Also, older females might enjoy the benefits of group living with minimized consensus cost by deciding the timing and direction of group travelling. Thus the protection provided by old females for younger ones might shape their age-ordered hierarchy and centrality among female bonobos.

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Chapter 1

General introduction

1. Female-female social bonding in non-human primates

Female-female relationships vary among group-living primates (reviewed by Sterck et al. 1997). Primarily, these relationships are explained by kin-selection (Silk 2002). Socioecological models predict that the strength of inter- and within-group competition, shaped by food quality and distribution, determines the structure of female social interactions in a species (Wrangham 1980; van Schaik 1989; Isbell & Vulen 1996; Sterck et al. 1997). In a highly competitive environment, related females should benefit from supporting each other to protect resources, both from other groups and non-kin members of their own group, thereby creating a selective pressure for staying with kin and leading the species to develop a female-philopatric society (van Schaik 1989; Isbell & Vulen 1996; Sterck et al. 1997). Females should engage in affiliative interactions frequently with their kin to maintain their supportive partnerships, in order to develop strong and nepotistic social bonding (van Schaik 1989; Isbell & Vulen 1996; Sterck et al. 1997). Even under situations with low competition, females still tend to stay in their natal group because of the cost of relocation and social reintegration (Isbell & Vulen 1996). However, without a selective pressure to support their kin and protect resources, females of these species are more likely to be egalitarian and non-nepotistic, and affiliative interactions are not expected to be frequent (Sterck et al. 1997).

These socioecological models explain well the observation that strong femalefemale bonding is found almost exclusively in female-philopatric and nepotistic species; however, there is one striking exception to this, and that is female bonobos which engage in strong social bonding in their *male*-philopatric society.

2. Female social bonding in bonobos and chimpanzees

The two species in the genus *Pan*, bonobos (*P. paniscus*) and chimpanzees (*P. troglodytes*), are closely related to each other and share basic socioecological characteristics. They both have stable, multi-male/multi-female social groups, in which males have a strong tendency to stay throughout their life, whereas females tend to leave their natal group around maturity (male-philopatric society). Both species feed primarily on ripe fruits and have a fission-fusion social style, where a group divides into several subgroups throughout the day ('parties': Nishida 1968; Kano 1982), although the patterns of fission-fusion are different for them (Furuichi 2009). Relative party size, or mean attendance ratio to observed parties of all adult individuals, is greater for bonobos than for chimpanzees.

The attendance ratio of female bonobos is equal or slightly higher than that of male bonobos while attendance ratio of female chimpanzees is much lower than that of male chimpanzees (Boesch 1996; Hohmann & Fruth 2008; Furuichi 2009). In addition, the membership of bonobo parties are often stable for days, whereas chimpanzees form more flexible parties with frequently changing of membership (Furuichi, 2009). These differences seem to be produced by the differences in female sociality between the two species (Furuichi 2009, 2011).

Socioecological models predict that both species should have weak female-female social bonding because of the male-philopatric nature of their societies. Although there exists inter-population variation (Lehmann & Boesch 2008), female relationships in chimpanzees conform well to these model predictions. In eastern chimpanzees, females tend to range alone with their offspring(s) or with a small number of females, except during estrus, and they seldom engage in affiliative interactions with other females (Goodall 1986; Pepper et al. 1999; Wrangham & Smuts 1980; Otali & Gilchrist 2005; Foerster et al. 2015; Hashimoto & Furuichi 2015; but see Langergraber et al. 2009). Western chimpanzee females are more gregarious, but female-female associations and affiliative interactions are still less frequent than those of the males (Boesch and Boesch-Achermann 2000; Lehmann & Boesch 2008; Wittiger & Boesch 2013).

In bonobos, however, the associations among females are as strong as, or stronger than that of males (Kuroda 1979; White 1988, 1998; Kano 1982, 1992; Hohmann & Fruth 2002; Furuichi 2009, 2011). While parties of chimpanzees are male-centric, those of bonobos are represented as 'female-centric' (Parish & de Waal 2000). White (1988) found that female bonobos remain gregarious even during periods of food scarcity, whereas the males tend to leave the large parties. The grooming interactions among females are as frequent, if not more, as those among males or between non-related males and females (Furuichi & Ihobe 1994; Furuichi 1997; Stevens et al. 2006). Furthermore, cooperative behaviors, such as coalitionary aggression and food sharing occur more frequently among females than among males (Stevens et al. 2006; Surbeck & Hohmann 2013; Yamamoto 2015). Taken together, these results indicate that female bonobos are gregarious, affiliative, and cooperative with each other. These characteristics in a male-philopatric society run counter to the predictions of socioecological models.

3. Why are female bonobos gregarious and affiliative toward each other?

Previous reports suggest that the high social status of female bonobos might be related to female gregariousness (Parish & de Waal 2000; Furuichi 2009, 2011). While all female chimpanzees are subordinate to adult males, female bonobos tend to possess an equal or

higher social status than males. As a result, female bonobos enjoy feeding priority over males, and are not subject to severe harassment by them either (Parish & de Waal 2000). Moreover, they seem to control the movement of the party, such that the party activity budgets are suitable for them (Furuichi 2009, 2011). Owing to these tendency, female bonobos tend to actively join a large party in order to enjoy the benefits of group living. The high social status of females may be established and maintained by female coalitions (Parish 1994, 1996; Vervaecke et al. 1999; Parish & de Waal 2000; White & Wood 2007; Furuichi 2011), and the need for forming a coalition might be the selective pressure that causes females to develop gregariousness and affiliative interactions (Parish 1996). However, these relationships among female social status, coalition, and affiliative interaction have not been evidenced by empirical studies to date.

4. Aim and outline of the thesis

The aim of my research was to study how female gregariousness and affiliative bonding evolved in the male-philopatric society of bonobos. Strong female social bonding is the key for understanding the gregarious nature of bonobos. Moreover, exploring the mechanism of their social bonding might give us cues for understanding the social bonding in unrelated female animals, including humans. In Chapter 2, I report a case, which demonstrates that bonobos have a strong motivation to maintain group cohesiveness. A large mixed-sex party of bonobos travelled a long distance to return to the location of a snare, apparently with the intention of searching for a fellow group member that had been caught in it.

In Chapter 3, I examine the patterns of female coalition formation. I first confirmed the context in which coalitions occur to understand the purpose of female coalition formation. Then, I tested the hypothesis that female affiliative interactions have evolved to facilitate coalition formation. The relationships between coalition formation frequency and the frequency of four affiliative measures (party association, proximity, grooming, and genito-genital rubbing) are investigated. I also examine whether agonistic support is reciprocal, and the benefits of forming coalitions for female bonobos. Through this chapter, I determine the role of coalition formation in the evolution of female gregariousness and occurrence of frequent affiliative interactions.

In Chapter 4, I investigate the leadership patterns in bonobos by observing their group movement coordination. I decided the individuals that determine the direction and timing of party departures when the group starts travelling (i.e. initiation; Pryitz 2011). I calculated the frequency of initiation for each individual, and examined whether their sex, age, dominance status, estrous state, and affiliative relationships affect this frequency. In

addition, I conducted individual-based analysis to see whether a specific individual(s) has the role of maintaining cohesiveness. Through this chapter, I aim to check whether female bonobos control the party movement.

In Chapter 5, I discuss the benefits for female bonobos to stay together, and how these benefits shape their sociality, for example, affiliative relationships and dominance hierarchy. This study sheds light on the structure of female-female relationships in wild bonobos and the putative reasons behind the 'female-centric' sociality observed in their male-philopatric society, which is essential for their social organization (Parish & de Waal 2000) but has not been systematically explained to date.

Chapter 2

Collective search for a lost member injured by a snare in wild bonobos at Wamba

1 Abstract

This is the first report to demonstrate that a large mixed-sex party of bonobos travelled a long distance to return to the location of a snare apparently to search for a member that had been caught in it. An adult male was caught in a metallic snare in a swamp forest at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo. After he escaped from the snare by breaking a sapling to which the snare was attached, other members of his party assisted him by unfastening the snare from lianas in which it was caught and licked his wound and tried to remove the snare from his fingers. In the late afternoon, they left him in the place where he was stuck in the liana and travelled to the dry forest where they usually spend the night. The next morning, they travelled back 1.8 km to revisit the location of the injured male. When they confirmed that he was no longer there, they returned to the dry forest to forage. This was unlike the usual ranging patterns of the party, suggesting that the bonobos travelled with the specific intention of searching for this injured individual who had been left behind. The incident described in this report

likely occurred because bonobos usually range in a large mixed-sex party and try to maintain group cohesion as much as possible.

2 Introduction

This is the first report of bonobos, or of any primates to the best of our knowledge, that a large party or group travelled a long distance to return to a particular location apparently to search for a lost member. In my study group of wild bonobos in the Luo Scientific Reserve, Democratic Republic of the Congo (DRC), bonobos are sometimes observed to be caught in snares. Although the use of traditional snares made from vines or nylon strings are allowed for subsistence hunting by local people living in the reserve, the use of metallic snares is prohibited. However, there are many instances in which people use metallic snares to trap bush pigs and large duikers. The metallic snare consists of a loop of iron wire and an arched sapling. When bonobos are caught in a snare, they are often able to free themselves by breaking a sapling to which the snare is attached, but it is difficult to remove fingers, hands, and feet from the wire. If the injury is too serious for the bonobo to continue following its party, the injured animal will likely be left behind (Furuichi 1999; B. Mulavwa, personal communication). These individuals are sometimes observed to rejoin their groups after their injuries have healed, but they may also die before doing so if their injuries are fatal. However, in the case of this report, an entire party travelled back to search for an injured member who had not yet rejoined it.

3 Methods

Bonobos have been studied at the Wamba field site located in the Luo Scientific Reserve (established in 1990) in DRC since 1973 (Kuroda 1979; Idani 1990; Kano 1992; Kano et al. 1996; Furuichi et al. 2012). From 1976 to 1991, researchers were aware of the presence of bonobos in PE group's current range, and at the time they named them "P group" (Kuroda 1979; Kano 1982; Idani 1990). Research at Wamba was disrupted because of political instability and re-started in 2003 with the continuous daily observation of P group's neighbor, E1 group. In September 2010, researchers started habituation and daily following in P group's old range, but because we could not immediately confirm whether it was the same group, we named them "PE group". After identifying individuals in PE group, we examined old photographs of P group taken before 1991. We found that two parous females, Yuba and Ruri, from P group (Idani 1990) were present in PE group, Bokuta and Kabo respectively. PE group is therefore likely to be the same P group that was studied pre-1991. In August and September 2011, the PE group consisted of five adult males (ML, GI, TK, SN, DN), seven adult females (Bk, Kb, Hd, Mt, Po, Ic, Sk), one adolescent female (Mr), and nine juveniles and infants. I and research assistants (I. Batuafe, B. Batuafe, E. Besao) followed a party of the PE group, and recorded its members using a 1-h party method (Hashimoto et al. 2001). We recorded the positions of the party at 1-min intervals using Garmin GPSMAP 60CSx. The party we observed during the particular morning of the observation described in this report included all members of the eastern subgroup except for one adult female (Mt) and her juvenile son.

4 Results

4 - 1 September 8, 2011

A party of 20 animals consisting of five adult males, six adult females, one adolescent female, and eight offspring was travelling to the south faster than usual (Figure. 2-1). As they frequently do, they seemed to be headed to a swamp forest to search for food. When they reached a place adjacent to the Luo River, where more than two thirds of the ground's surface was covered with running water due to heavy flooding, they stopped proceeding and returned about 50 m to the north, where they ate fruit of *Julbernadia seretii* for a short time and then took a long rest. *Julbernadia* was a plant that they could find abundantly in other places. After this rest, they resumed ranging to the north-west.

At 13:15, we heard screams coming from a place near where the party was resting. We located the place at 13:16 and found an adult male, Malusu (ML), crouching on the ground. He seemed to have broken a sapling to which a metal wire had been attached and had run away from the place with the wire still ensnaring his fingers. We searched for the broken sapling in the immediate vicinity but could not find it. Seven other bonobos, TK, SN, GI, Kb, and Hd and two offspring, had gathered around him and some were touching his back, but he was not moving. We touched him by using a long stick to confirm whether he was still alive, and he stood up. TK and SN barked and shook branches to threaten us. The looped metallic wire had ensnared the second to fifth fingers of his wright hand. At the other end of its 30-cm extension, the wire was connected to a 30-cm stick that was a part of the sapling to which the wire had been attached (Figure 2-2). The stick was stuck in lianas, which prevented ML from moving. TK unfastened the stick from the liana, and ML climbed up about 4 m on an adjacent small tree.

It started to rain heavily at 14:04. ML was resting on the tree. Six individuals including TK, SN, Bk, and Po were resting about 10 m away from ML. Other individuals had already left to return to the dry forest in the north. Although bonobos living in this area sometimes sleep in the swamp, they usually return to the dry forest in the evening (Kano 1992; Mulavwa et al. 2010). It stopped raining at 15:00. BK approached ML and watched him at a distance of 1 m, but she did not touch him. ML climbed down from the tree at 15:24 and tried to move on the ground, but the stick attached to the wire got stuck in lianas again. We cut the liana twice to enable ML to move. This time, the other individuals did not threaten us. ML climbed up 5 m on a tree and got caught in liana again.

TK, SN, and Bk approached ML. Bk sniffed at the wire. TK tried to remove the wire from ML's hand, but he was not successful. SN removed the stick from the liana, but still the wire was caught in another liana. They watched ML at a distance of 3 m.

TK, SN, Bk, and Po climbed down from the trees at 16:00 and left the site to follow the other members to the sleeping site in the north. We also left ML and followed the other individuals because we could not stay in the swamp area late in the evening. They travelled back exactly the same way as they had come in the morning, moving approximately 1.8 km to join the other members to sleep.

4 - 2 September 9, 2011

At 07:10, part of our research team arrived at the site where we had last seen ML. He was no longer there, and we concluded that he had likely escaped from the lianas. We searched the vicinity for half an hour but could not find him. Another part of our research team arrived at the northern sleeping site at 05:59. The bonobos awoke and started travelling at 06:22. By listening to their contact calls, we knew that they had split into two parties. One party travelled to the east, and the other travelled to the south. We followed the former, which consisted of TK, Kb, Po, Mr, and three offsprings. They fed on fruit of *Anonidium manni* and *Landolphia owariensis* intensively until they made day nests and rested at 07:28.

At 08:35, we heard long-distance calls from the southwest. The party we were observing answered the calls and started travelling toward them at 08:45. When the two parties joined each other, we counted 15 animals consisting of TK, GI, SN, Bk, Kb, Hd, Po, Sk, Mr, and six offspring. This was almost the same composition as the party we observed when ML was caught in the snare, except for the absence of DN, Ic with two offspring, and ML himself. The newly merged party entered the swamp at 09:36 and continued travelling very quickly without feeding or resting, using the same route that they travelled the previous evening.

We followed their tracks and at 10:22 passed the place where ML had been left alone the previous day. The tracks continued another 50 m, and at 10:27, we found bonobos resting. We found a broken sapling and a small hole beside it. It seemed to be the remnants of the snare that had caught ML because it had been broken very recently. We also found another intact metallic snare in the vicinity. Three females were feeding on young beans of *Gilbertiodendron dewevrei* but not intensively. Shortly, at 10:43, the group started travelling quickly to the north and left the swamp. We finished following them at 12:00.

4 - 3 ML's absence and return in the large party

ML was not found after these incidences, though parties of the PE group were being observed on a daily basis. However, we spotted him in a party of PE group on 21 and 22 October. His fingers were still ensnared and he could not move his hand, but he could climb trees, feed, and travel with other members. After these two days, ML again disappeared. He returned to the party on 3 December and has been observed daily basis since then (Figure 2-3).

5 Discussion

It have been frequently observed the bonobos in Wamba to show interest in the injury of other group members. In one instance, an adult male licked a wound on his foot probably received during an antagonistic interaction. A young adult female approached him and also licked his wound (T. Furuichi, personal communication). Such behavior has been observed between many age–sex combinations. Although there are few reports of one animal licking wounds on another, it is a common behavior for chimpanzees (Nishida et al. 1999; Amati et al. 2008; K. Hosaka and K. Zamma, personal communication).

Attempts to release other animals from snares or remove wire from the fingers or hands of other animals have also been observed in both bonobos and chimpanzees. Furuichi observed an instance in which at least two adult and two adolescent females and one infant in the E1 group of bonobos reached out their hands to, smelled, and licked the wounds of, another adult female (Km), whose fingers were ensnared in metallic wire. One of the females reached for the stick to remove it, but Km fled from her, likely because of the pain (Furuichi 1988). Mulavwa observed another instance in E1 group, in which a female (SI) released her infant male (SB) from a snare made from nylon by cutting the vine that connected the nylon snare to a sapling (B. Mulavwa, personal communication). Thus, my observation in PE group was the third such observation at our bonobo study site. In chimpanzees, a successful case of snare removal was reported from the Sonso community in the Budongo Forest (Amati et al. 2008). When an adult female was caught in a nylon snare, an alpha male broke the sapling to which the wire was attached and later removed the wire from her hand using his teeth. Otherwise, there have been no other reports of attempts by one animal to remove snares from another animal's hands or fingers, despite the large number of cases of animals caught in snares and experiencing snare injury that have been reported at many study sites (Hashimoto 1999; Boesch & Boesch-Achermann 2000; Waller & Reynolds 2001; Quiatt et al. 2002; Reynolds 2005; Ohashi & Matsuzawa 2011). One reason for the lack of such reports is that chimpanzees that tend to range alone or in small parties (Furuichi 2009) may be less likely to be observed when

caught in snares.

A unique aspect of this case study is that bonobos were observed travelling a long distance in order to return the following morning to the site where one of their members was injured. As far as I know, there has been no such report on any primate species. Although I could not observe actual searching behavior, because I followed the group's tracks and arrived late at the site where ML had been ensnared, I can infer that they went back to find him for two reasons: First, they did not visit the same place in order to find food. They returned by way of the same route as they had come the previous evening without feeding on anything, and when they arrived, only a few members fed quickly on some fruit that they could have found elsewhere. They knew that there was no attractive food there because they had visited the same place in a vain search for food on the previous day. Therefore they seemed to return to the place for a reason other than finding food, most likely to search for ML. Second, the bonobos stopped their rapid travel at the place where ML had been caught in the snare. After they passed the place where ML was left the previous evening, they continued another 50 m to where the broken sapling had been located. After they did not find him, they returned north after a short break, suggesting that they visited the area only to search for ML. There is a report that a male chimpanzee in Bossou, Guinea, deactivated snares intentionally (Ohashi & Matsuzawa 2011). Judging from the injuries on their hands, at least two members of the PE group of this report (GI and HD) had been caught in a snare in the past. Therefore, it is possible that bonobos of this particular group might understand the causal relationship between the snare and the loss of ML.

The following morning, the sleeping party split into two, and one started travelling back to the place where ML had been left. Probably, one or more bonobos in the party noticed the absence of ML and had a strong motivation to look for him. The most likely candidates are Bk and SN. In previous day, Bk, Po, SN, and TK stayed with ML longer than other individuals. Bk and SN were in the party which first started travelling back to the place where ML had been left. Although the other party originally moved to a different direction to feed, they immediately joined Bk and SN's party when members called them. I can therefore infer that many of the party members recognized the common purpose of their rapid travel to the south.

Another unique aspect of this case study is that a large party of bonobos travelled back to search for a lost member. This likely comes from a strong tendency of bonobos to form a mixed-sex party and to maintain group cohesion (White 1988; Kano 1992; Furuichi 2009; Furuichi 2011). In chimpanzees, some animals stay with injured or sick animals (Goodall 1986; K. Hosaka, personal communication). Although some individuals may return to look for a lost animal left behind (Huffman 1989), it is unlikely that an entire party would do so together because chimpanzees form flexible parties that may easily split into several parties or individuals who have different destinations (Nishida 1968; Wrangham 1979; Hashimoto et al. 2001; Furuichi 2009). Bonobos show a much higher ratio of attendance to mixed-sex parties than do chimpanzees, and various behaviors suggest that they are highly motivated to range together with other members to maintain group cohesion. For example, they do not start travelling until they agree on a common direction of travel, and they also wait for other parties that are following behind during long distance travel (Kano 1992; Furuichi 2009; Furuichi 2011). Also, parties within the same vicinity call in the evening to invite each other to sleep together (Kuroda 1979; Kano 1992; Mulavwa et al. 2010). In the studied case, four individuals who stayed with ML until the evening finally left him to join the other members to sleep together, suggesting that they were strongly motivated to stay with the other members, though they returned the next morning to the place at which they had left ML.



Figure. 2-1 The ranging route of the party of PE group on 8 and 9 September 2011



Figure 2-2: A metal wire and an arched sapling

A young female (Pf) of E1 group holds a metallic wire that had ensnared the fingers of

her left hand. It features the same type of snare described in this study



Figure 2-3: The picture of ML in 2015.

Although his right hand has been deformed, he seems to live without great inconveniences.

Chapter 3

Patterns of female coalition formations in wild bonobos at Wamba

1 Abstract

Patterns of coalitionary aggression among female animals are generally explained by kinselection theory. Frequent female coalitions are almost exclusively observed in femalephilopatric species, where females stay in their natal group, and females typically form coalitions with their kin. Bonobos (Pan paniscus), in contrast, are male-philopatric, with females immigrating to new groups at adolescence, but female bonobos frequently form coalitions even though they are generally with non-relatives. Here I investigated the patterns of female coalitions in a group of wild bonobos at Wamba, Democratic Republic of the Congo, in order to explore alternative mechanisms to kin-selection for cooperation among females. I found that all female coalitions (defined as coalitions in which two or more females participated) were formed to attack males, usually after the male(s) behaved aggressively toward one or more females. There was no evidence that female bonobos used proximity, grooming, or genito-genital rubbing (GG-rubbing) to develop coalition partnerships, although higher association provided females with more opportunity to form coalitions. Instead of reciprocal agonistic support, I found a uni-directional relationship in which older females supported younger females. Females won against males more easily when they formed coalitions than when they confronted males alone. Unlike female coalitions in other species that use coalitions to cope with competition among females, my results suggest that coalitions in female bonobos might have evolved as a counterstrategy against male harassment. Females might choose their coalition partners based not on affiliative relationship or reciprocity but on mutualism. Directly inverse to the hypothesis that affiliative behavior leads to coalition formation, coalitions might in fact enhance gregariousness among females, leading females to develop affiliative interactions that promote for tolerance.

2 Introduction

Cooperation is widespread in the animal kingdom, ranging from cooperative breeding (Clutton-Brock 2002; Wong & Balshine 2011); to food-sharing (Carter & Wilkinson 2013); to allogrooming (Pettis & Pankiw 1998; Schino & Aureli 2008); to coalitionary aggression. Coalitionary aggression, hereafter referred to as 'coalition(s)', involves two or more individuals cooperating to attack a common conspecific target (Harcourt & de Waal 1992; Bisonnette et al. 2015), and is observed in species that engage in complex ingroup social relationships. The choice of coalition partner is not random (reviewed in Smith et al. 2010); rather, patterns of intra-group coalition formation are explained by kin-selection (Hamilton 1964; Silk 2002), reciprocity (Trivers 1971), and mutualism (West-Eberhard 1975; Bercovitch 1988). Previous studies on primates (reviewed in Sterk et al. 1997; Silk 2002, 2006; Kapsalis 2004) and other social living animals (reviewed in Smith et al. 2010; Smith 2014) have revealed that a general pattern of coalition formation among females is well explained by kin-selection theory. Female-female coalitions were observed almost exclusively in female-philopatric species, where females stay within their natal groups, and primarily among close kin (Sterck et al. 1997; Silk 2006; Smith et al. 2010). Female affiliative interactions and coalition formation are largely biased towards kin and are stable for long periods. Such a long-term relationship, characterized by repeated coalition formation and high levels of affiliation, is called an 'alliance' (Bisonnette et al. 2015).

In evolutionary models, alliances among kin are among the most important factors shaping female social relationships in primates (Wrangham 1980; van Schaik 1989; van Hooff & van Schaik 1992; Sterck et al. 1997). In a highly competitive environment, related females should benefit from supporting each other to protect resources, thereby creating a selective pressure for staying with kin and leading the species to develop a female-philopatric, nepotistic society. In situations with low competition, without selective pressure to support kin, females are more likely to disperse and their society will be non-nepotistic. The socioecological models successfully explains why frequent female coalitions are observed almost exclusively in female-philopatric species, and why they form alliances with their kin. However, there is a striking exception that does not fit the model: female bonobos (*Pan paniscus*) form coalitions frequently (Parish 1996; Stevens et al. 2006; Surbeck & Hohmann 2013) even though the coalitions are generally between non-relatives because of their female-dispersing society (Kano 1992; Hashimoto et al. 1996; Gerloff et al. 1999; Eriksson et al. 2006; Sakamaki et al. 2015). If the kin-selection model, which explains female coalitions so well in other species, can't explain coalitions for female bonobos, then why and how do female
bonobos form coalitions without kin? Bonobos provide a precious opportunity to understand the mechanism of cooperation among females without direct kin-selection.

Chimpanzees and bonobos are very closely related. Both live in multimale/multi-female groups and have a fission-fusion social system in which a group splits into temporary subgroups (called 'parties': Nishida 1968; Kano 1982). Additionally, both species have a strong female-biased dispersal pattern (Nishida 1979, Kano 1982, 1992; Goodall 1986; Eriksson et al. 2006; Sakamaki et al. 2015), although the tendency of female dispersal may be stronger in bonobos – female chimpanzees occasionally stay in their natal group (Goodall 1986; Nakamura 2015; Foerster et al. 2015), and such a case has not yet been reported in bonobos. Despite these similarities in basic social structure, chimpanzees and bonobos show a considerable difference in their patterns of coalition formation.

Social bonds in female chimpanzees are known to be weak, though there is interpopulation variation in female sociality (Lehmann & Boesch 2008). In eastern chimpanzees, females tend to range alone with their offspring(s) except during oestrus, and they seldom engage in affiliative interactions (Goodall 1986; Pepper et al. 1999; Wrangham & Smuts 1980; Otali & Gilchrist 2005; Foerster et al. 2015; Hashimoto & Furuichi 2015; but see Langergraber et al. 2009). Western chimpanzee females are more gregarious, but female-female associations and affiliative interactions are still less frequent than those of males (Boesch & Boesch-Achermann 2000; Lehmann & Boesch 2008; Wittiger & Boesch 2013). Female coalitions are rare (Newton-Fisher 2006), but have been reported at some field sites where females are more gregarious (Tai and Budongo: Boesch & Boesch-Achermann 2000; Newton-Fisher 2006) and also in captivity (de Waal 1984; Baker & Smuts 1994).

Male chimpanzees engage in strong, durable affiliative relationships and frequently form coalitions (Nishida & Hosaka 1996; Boesch & Boesch-Acherman 2000; Mitani 2009). Forming coalitions provides chimpanzee males with direct fitness benefits such as rank improvement and increased number of offspring (Gilby et al. 2013). Early research explained their coalitions by kin-selection (Goodall 1986), and later empirical studies expounded that they form coalitions with both close and distant relatives when they are able to gain benefits from the coalition (Langergraber et al. 2007; Mitani et al. 2000). Although the formation of coalitions is often temporary and flexible (de Waal 1982, 1984; Boesch & Boesch-Acherman 2000), males choose coalition partners based on their daily social relationships and reciprocity. Males who are more frequently associated spatially and who groom each other are more likely to form coalitions (Nishida 1983; Hemelrijk & Ek 1991; Watts 2002), and they support each other reciprocally (Watts 2002; Mitani 2006; de Waal & Brosnan 2006). Some male dyads form alliances, which can sometimes last for years (de Waal 1982; Nishida 1983; Nishida & Hosaka 1996; Watts 2002; Gilby & Wrangham 2008; Mitani 2009).

In wild bonobos, affiliative relationships among males are weaker than in male chimpanzees, and male bonobos seldom form coalitions (Ihobe 1992; Furuichi & Ihobe 1994; Surbeck & Hohmann 2013). Female bonobos, on the other hand, are much more social than female chimpanzees and tend to range in large mixed-sex parties, keeping close association with other individuals (Kuroda 1979; White 1988, 1998; Kano 1992; Furuichi 2009, 2011; Hohmann & Fruth 2002). Grooming interactions among female bonobos are as frequent as or more frequent than among males or between unrelated males and females (Furuichi & Ihobe 1994; Furuichi 1997; Stevens et al. 2006). Moreover, females form coalitions more frequently than do males (Stevens et al. 2006; Surbeck & Hohmann 2013).

The social status of female bonobos is equal to or higher than that of males, and females have feeding priority (Furuichi 1997, 2011; White & Wood 2007; Surbeck & Hohmann 2013). Female rank and social-centrality is thought to be acquired and maintained by female aggregation and coalitions (Parish 1994, 1996; Vervaecke et al. 1999; Parish & Waal 2000; White & Wood 2007; Furuichi 2011). Researchers have proposed that affiliative interactions among female bonobos, especially genito-genital or "GG"-rubbing (Kuroda 1980), have evolved to promote coalition formation (Parish 1996). However, one study on wild bonobos at Lui Kotale did *not* find a tendency for females to choose close associates or GG-rubbing partners as coalition partners (Surbeck & Hohmann 2013).

In this way, female coalitions have been considered paramount for shaping the social lives of bonobos. Despite their apparent importance, there have been few systematic studies on coalition formation in bonobos (Stevens et al. 2007). Do female bonobos form coalitions based on their affiliative relationships and reciprocity, as male chimpanzees do? The aim of this study is to clarify the pattern of coalition formation and investigate the factors that promote coalition formations among wild female bonobos. I first investigate the size, target, and context of female coalitions. I then examined whether daily affiliative relationships promote coalition formation and whether agonistic support is reciprocal. Additionally, I examined the potential risks and benefits for female bonobos by forming coalitions.

3 Methods

3-1 Study site and subjects

Observations were conducted on wild bonobos, PE group, at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo, where long-term research has been conducted since 1974 (Kano, 1992). From 1976, researchers were aware of the presence of bonobos in PE group's current range, and at the time they named them "P group" (Kuroda 1979; Kano 1982; Idani 1990). Research at Wamba was disrupted in 1996 because of political instability and re-started in 2003 with the continuous daily observation of P group's neighbour, E1 group. In September 2010, researchers started habituation and daily following in P group's old range, but because we could not immediately confirm whether it was the same group, we named them "PE group". After identifying individuals in PE group, we examined old photographs of P group taken before 1991. We found that two parous females, Yuba and Ruri, from P group (Idani 1990) were present in PE group, Bokuta and Kabo (Table 3-1) respectively. PE group is therefore likely to be the same P group that was studied pre-1996.

At the time of the present study, PE group consisted of 26–27 individuals. All individuals were identified and habituated from the beginning of the study period. My study subjects were mature individuals who were older than 8-years-old, but I excluded one female who emigrated during the study period (15 indivuals: 9 females and 6 males, Table 1).

Data on females who temporarily visited this group were not analyzed. I estimated the age of subject animals based on their physical features. Individuals estimated to be 35 years old or more were classified as old, and individuals from 21 to 34 years old were classified as middle aged. Individuals less than 21 years old were classified as young. I could not confirm the linear dominance relationship for females because aggressive interactions among them were very rare (28 dyadic aggressive interactions among only 12 dyads of 36 female-female dyads). However, social rank and age are strongly correlated in wild female bonobos in that older females are higher ranking than younger ones (Furuichi 1989, 1997), and all of my female-female dyadic aggression data also followed this tendency.

3-2 Behavioral Observation

Bonobos were observed for a total 1889 hours with two local assistants from June to November, 2012; August, 2013 to January, 2014; July to September, 2014; and January to June, 2015. I recorded all observed intra-group aggressive interactions, which by definition, included at least one aggressive behavior. Aggressive behaviors were as follows: vocal or non-vocal threatening, directed displaying, charging, chasing, and physical attack (kick, beat, grabbing, etc.). Submissive behaviors were as follows: avoiding, jumping aside, fleeing, grimacing, and screaming. When at least one submissive behavior was observed, I judged that the submissive individual had lost the aggressive interaction. When both individuals grimaced or screamed, the individual who fled from the opponent was considered the loser. There was no case in which all individuals grimaced or screamed and none or both of them fled. If two or more individuals jointly attacked one or more common target(s), I recorded the attack as a coalition (Harcourt & de Waal 1992). Coalitions in which two or more females participated were termed 'female coalitions'. I recorded the direction of agonistic support only when I could clearly identify the supporter(s) and receiver(s). Frequency of coalition formation of a dyad (A & B) was calculated as follows (Cairns & Schewager 1987):

$$Co(ab) / (Ag(a) + Ag(b) - Ag(ab))$$

Co(ab) = number of coalitions A and B both attended on the same side

Ag(a) = number of aggressions A attended

Ag(b) = number of aggressions B attended

Ag(ab) = number of aggressions A and B both attended

The affiliative relationship of each female–female dyad was evaluated using 4 measures: frequency of (1) attendance in the same party, (2) spatial proximity, (3) grooming interactions, and (4) GG-rubbing. Party composition was recorded by the one-

hour party method; defined as the individuals who were observed in hourly during the observations comprised the party members of the hour (Hashimoto, Furuichi, & Tashiro, 2001). I also recorded grooming interactions and spatial proximity by instantaneous scan sampling (Altmann 1974); at 5 minute intervals and for all visible individuals, I recorded whether they were in close proximity (less than 3 m) or grooming with any other individuals, although proximity was not recorded when the general behavior of the party was traveling because of the difficulty of recording precise data. I collected 5079 \pm 1253 scan samples per subject female (average \pm SD). GG-rubbing was observed *ad libitum* (Altmann 1974). For each measures, I calculated the strength of a dyad (A & B) as follows (Cairns & Schewager 1987):

- 1. Same-party attendance index (ab) = Pa(ab) / (Pa(a) + Pa(a) Pa(ab))
- Pa(ab) = number of parties containing both A and B
- Pa(a) = number of parties containing A
- Pa(b) = number of parties containing B
- 2. Proximity index (ab) = Pr(ab) / Sc(ab)

Pr(ab) = number of scans in which A and B were within 3m of one another

Sc(ab) = number of scans containing both A and B

3. Grooming index (ab) = Gr(ab) / Sc(ab)

Gr(ab) = number of scans in which A and B engaged in grooming interactions
4. GG-rubbing index = GG(ab) / Pa(ab)
GG(ab) = number of GG-rubbing events between A and B

3-3 Data Analysis

I used R 3.1.2 for all statistics except for analysis of reciprocity of agonistic support, in which case I used MATSQURE (Hemelrijk, 1990a).

I ran a generalized linear mixed model (GLMM, package 'lme4'; Douglas et al. 2012) to assess the relationship between sex combinations and frequency of coalition formations, using the coalition frequency as the dependent variable, using 'cbind function' and the error distribution 'binomial'. I entered the sex combination of each dyad as a fixed factor. Identity of the individuals in the dyad were used as random effects to take into account individual differences. I ran another GLMMs to assess the relationship between female's affiliative relationships and frequency of coalition formations. I used the frequency of coalition formation of female dyads as the dependent variable, using 'cbind function' and the error distribution 'binomial'. I entered the same-party attendance index, proximity index, grooming index, and GG-rubbing index of each female dyad as a fixed factor in each model. Identity of the individuals in the dyad was used as random effects.

Prior to the analysis, I checked the distribution of the predictors and square-roottransformed 'grooming index' and 'GG-rubbing index' to achieve approximate normality.

A Kr matrix correlation test was used to examine reciprocity of given and received agonistic support using Hemelrijk's MATSQURE (Hemelrijk 1990a). This test analyses group-level reciprocity by calculating the correlation between a supporter– receiver matrix and its inverse.

4 Results

4-1 Sex Combination of Dyads and Frequency of Coalition Formation

I observed 699 separate aggressive interactions (403 male–male, 28 female–female, and 268 intersex). 108 coalitions were observed; 58 coalitions were formed only by females and 9 only by males, and 41 coalitions were formed together by female(s) and male(s). The frequency of coalition formation was significantly more frequent in female–female dyads than in female–male or in male–male dyads (GLMM, number of pairs = 105, Table 3-2: Model 1, Figure 3-1).

4-2 Size, Target, Severity, and Context of Female Coalitions

Two or more females took part in 73 coalitions. Of those coalitions, 15 included one or

more males. Each female coalition contained 2.72 ± 0.97 individuals on average (2–6 individuals, 2.44 females and 0.28 males). All of the targets of female coalitions were male(s), of which most (95.5%) were adult. Females *never* formed coalitions to attack other females. Only four female coalitions (5.5%) involved just threatening, while 55 (75.3%) involved charging or chasing. Females engaged in physical attacks in 14 female coalitions (19.2%), and in one case the target male was injured – he lost the tip of his forefinger on his right foot.

Fifty female coalitions (68.5%) were formed during or immediately after a male's aggressive behavior or undirected display towards or around one or more females. Nine (12.3%) were formed to aid a male during a male–male aggression, and 1 (1.37%) was formed toward a male who was persistently soliciting copulation. The provocation was not known for another 13 coalitions.

4-3 Female–Female Affiliative Relationship and Coalition Formation

Dyads of females with a higher same-party attendance index formed coalitions more frequently (GLMM, number of pairs = 36, Table 3-2: Model 2, Figure 3-2a). However, proximity, grooming, and GG-rubbing indices did not correlate significantly with frequency of coalition formation (GLMM, number of pairs = 36, Table 3-2: Model 3, 4, 5, Figure 3-2b, c, d).

4-4 Direction and Reciprocity of Female Agonistic Support

Direction of agonistic support was known in 47 female coalitions, but 9 coalitions in which females supported a male were excluded. These coalitions were divided into 54 supporter–receiver interactions. There was a significant negative relationship between support given and support received (tau Kr-test, 2000 permutations, Tau Kr = -0.38, p = 0.026, Figure 3-3). Therefore, the agonistic support was not reciprocal. Moreover, the negative correlation indicates that individuals who frequently gave support tended not to receive support and vice versa. Table 3-3 shows the matrix of agonistic supports.

Apparently, the exchange of agonistic support between individuals within dyads was strongly biased to one side of the dyad. Forty-four supports (81.5%) were given across different age categories (Table 3-4). Supports were more directed from females of older age categories to younger age categories (95.5%) than vice versa (4.5%) (binomial test, df=1, N = 44, p < 0.01).

4-5 Risks and Benefits of Forming Female Coalitions

Since female coalitions were only directed toward males, I considered the result of inter-

sex aggression here. I observed 199 dyadic inter-sex aggressions. Of those, submissive behavior(s) was observed in 152 aggressions. Of 152 decided dyadic intersex aggressions, females won 105 (68.9%), and males won 47 (31.1%). Old females were more likely to win conflicts against males than were young females (old females; 84.0%, middle-aged females; 69.5%, young females; 29.3%, chi-squired multi-comparison test using Ryan method, a significant difference was detected only between old females and young females, df = 2, p < 0.01). When females formed coalitions, 100% (N = 73) won against target male(s). I never observed target male(s) opposing female coalitions, and females never got injured during coalition events. The winning rate was higher in any age category when females formed coalitions than when they did not (Mantel-Haenszel chi-squared test, old: $X^2 = 11.55$, df = 1; p < 0.01, middle-aged: $X^2 = 19.64$, df = 1, p < 0.01; young: $X^2 = 21.37$, df = 1, p < 0.01. Figure 3-4).

5 Discussion

I investigated patterns of coalition formation in female bonobos. Female bonobo social relationships are unusual in that they have strong female social bonding within a female-dispersal society. In this study, female-female dyad coalitions were formed more frequently than male-male dyads and male-female dyads, as previously confirmed in

other studies (e.g. Stevens et al. 2006; Surbeck & Hohmann 2013).

In other species, female coalitions are generally used for female–female competition, to maintain social status, or to usurp valuable food resources among females (Sterck et al. 1997; Isbell & Young 2002; Silk et al. 2004; Smith et al. 2010). However, in this study, female bonobo coalitions were never directed toward other females. All female coalitions were directed toward males, especially when the male was behaving aggressively toward females. Females were tolerant of each other, and aggression among females was rare. Similarly, in captive bonobos, female–female aggression seldom elicited support from other individuals (Vervaecke et al. 2000c). These results suggest that female coalitions have evolved as a strategy not to cope with competition among females but, rather, to cope with inter-sex competition, i.e. to prevent harassment by males.

Although females of other non-human primates typically form coalitions with their close kin, there are episodic examples of unrelated females cooperating to attack a male (reviewed by Smuts & Smuts 1993; see also Setchell et al. 2006). This kind of female coalition may benefit *all* females by detering all males from attacking females because of the risk of counter-aggression from female coalitions (Smuts & Smuts 1993; Setchell et al. 2006). Sterck et al. (1997) did not support the hypothesis that female coalitions evolved as a strategy to counter male harassment in non-human primates, since establishing good relationships with males might be more effective. However, coalitions of female bonobos have been considered to be useful for preventing male harassment (Kano 1992; Parish 1994, 1996; Hohmann & Fruth 2003; White & Wood 2007; Furuichi 2011), and my results support this view.

This does not mean that female bonobos devote less effort to establishing good relationships with males. Female bonobos groom unrelated males as frequently or more frequently than they do other females (Furuichi & Ihobe 1994; Hohmann et al. 1999; Stevens et al. 2006). Female bonobos suffer little from male harassment since they receive neither severe aggression from males (Furuichi 1997, 2011; Vervaecke et al. 1999; Hohmann & Fruth 2003) nor infanticide (Wilson et al. 2014), whereas female chimpanzees do suffer from these (Hamai et al. 1992; Muller et al. 2009; Wilson et al. 2014; Feldblum et al. 2014). Using both strategies—coalitions among females against males and establishing good relationships with males—female bonobos might effectively prevent harassment by males.

I found that female dyads with a higher same-party association formed coalitions more frequently. However, spatial proximity and grooming were not significantly correlated with coalition formation. Perhaps surprisingly, the frequency of GG-rubbing, which is proposed to promote female-female social bonding and coalition formation (Parish 1996; Paoli et al. 2007), did not have a significant effect on coalition formation either, corroborating findings at Lui Kotale (Surbeck & Hohmann 2013). These results indicate that presence in the same party is more important for coalition formation than specific affiliative behaviors.

Even though females did not choose their close 'friends' as coalition partners, affiliative interactions might enhance female coalitions. Affiliative interactions may be exchanged for tolerance. Grooming is exchanged for tolerance during feeding in several primate species (rhesus macaques: Kapsalis & Berman 1996; Japanese macaques: Ventura et al. 2006; Barbary macaques: Carne et al. 2011; tufted capuchin monkeys: Tiddi, et al. 2011). Although GG-rubbing in female bonobos is multi-functional (Hohmann & Fruth 2000), it occurs most often during feeding and may reduce tension and enable females to co-feed (Kuroda 1980; Furuichi 1989; Parish 1994; Hohmann & Fruth 2000; Fruth & Hohmann 2006; Paoli et al. 2007; Ryu, Hill, & Furuichi, 2015). These affiliative interactions might enable females to tolerate one another and to be in the same party, thereby indirectly contributing the formation of female coalitions.

Reciprocal agonistic support is observed in several animal species (e.g. bonnet macaques: Silk 1992; chimpanzees: Watts 2002; Mitani 2006; coatis: Romero & Aureli 2008; ravens: Fraser & Bugnyar 2012). The agonistic support of bonobos in 5 captive groups was highly reciprocal at the group level, but the result was mostly a side effect of strong correlations between support and dominance (Vervaecke et al. 2000b; Stevens et al. 2005). Reciprocal exchange of support was found only in one group after controlling for rank effect (Vervaecke et al. 2000b; Stevens et al. 2005). In this study, wild female bonobos did not support each other reciprocally. These tendencies might indicate that reciprocal altruism had little effect on the evolution of female coalition in bonobos. Nonreciprocal support may be due to uni-directional relationships within a dyad in which older females support younger ones.

In this study, all observed female coalitions resulted in the target male displaying submissive behaviors. Females of all age categories could win against males more easily when they formed coalitions than when they confronted males alone. This benefit of forming coalitions might be greater for young females than for old females since young females were less likely to win against males in dyadic aggression than were old females. Furthermore, female coalitions may benefit all females by making males refrain from attacking females because of the risk of counter-aggression (Smuts & Smuts 1993). Participating in female coalitions might be a low-risk behavior because males never opposed female coalitions. Since all females in the coalition gained benefits from forming coalitions, female coalitions might be formed for mutual individual benefits (or mutualism: Clutton-Brock 2009).

Uni-directional agonistic support from older to younger females might be explained by benefits to both females. For younger females, who might find it difficult to dominate males if they confront males by themselves, agonistic support from older females might enable them to stay central to the party without suffering male harassment. Since older females tend to be dominant and stay in the best feeding positions (Parish 1994; Furuichi 1989, 2011), young females may experience feeding disadvantage to some extent. However, the benefit of receiving agonistic support might enhance the advantage of associating with older females, including feeding priority over males (Parish 1994; Furuichi 1997; White & Wood 2007), thereby compensating for the feeding disadvantage among females. Some behaviors of young females indicate that they are attracted to older females; young females associate with and follow older females actively (Idani 1991; Sakamaki et al. 2015) and beg for abundant fruit from them to confirm their tolerance (Yamamoto 2015; Goldstone et al. 2016).

On the other hand, for older females, attracting younger females around them might be beneficial in enhancing the mating success of their sons, since a male's mating success is higher when his mother is in the same party (Surbeck et al. 2011). It might also be the reason why old females stay in the central part of the party (Furuichi 1989, 2011; Parish 1996) and control party movement (Furuichi 2009, 2011; Chapter 4). Old females might actively support younger females not only because they gain the direct benefit of winning against males but also because they are able to enhance the benefit of groupliving by attracting other females around them.

The results suggest that female coalitions in bonobos might have evolved as a counterstrategy against male harassment. Females might choose their coalition partners based not on affiliative relationship or reciprocity but, rather, on mutualism. The importance of coalition partners largely affects the shape of female social relationships in non-human primates (Wrangham 1980, van Schaik 1989; van Hooff & van Schaik 1992; Sterck et al. 1997). Additionally, in bonobos, female coalitions might lead to the development of affiliative behaviors and high tolerance among females. There may be positive feedback between female coalition formation and female gregariousness, wherein the benefits of forming coalitions may enhance gregariousness, and gregariousness promotes the formation of female coalitions. There may be additional positive feedback between female gregariousness and female affiliative interactions for tolerance, where the importance of being gregarious might lead females to develop tolerant behaviors (i.e., GG-rubbing and frequent grooming among females). Although there was no direct connection between affiliative behaviors and coalition formation, the strong female social bonds in female-dispersal societies might have been established and reinforced by these positive feedbacks. When male efforts to dominate or coerce females were no longer useful due to female resistance, males might have had to develop good relationships with their mothers and other females to attain mating success rather than behaving aggressively toward females (Furuichi 1989; Kano 1992, 1996; Surbeck et al. 2011; Hare et al. 2012).

Although wild female chimpanzees rarely form coalitions, female coalitions are observed relatively often at some sites where females are more gregarious (e.g. Boesch & Boesch-Achermann 2000; Newton-Fisher 2006). The pattern of female coalitions observed in Budongo forest chimpanzees is very similar to my results. Newton-Fisher (2006) observed 9 female coalitions retaliating against male harassment. Most agonistic support was directed from dominant females toward subordinate females, suggesting that there might not be a reciprocal relationship. These similarities suggest that patterns of female coalitions might not have evolved specifically in bonobos but, rather, are common among *Pan* species.

Variation in female gregariousness, which may be caused by food abundance, could be pivotal to promoting or constraining female coalitions (Parish 1996). Great behavioral diversity is reported within the genus *Pan* (Whiten et al. 1999; Boesch,

Hohmann, & Marchant 2002). Most studies of wild bonobos, including ours, have been conducted in dense forest habitats where food availability is relatively high and stable (White & Wrangham 1988; White 1998). However, bonobos live in diverse environments, including mosaic forests where conservation, habituation, and research activities have begun quite recently (Inogwabini et al. 2008; Serckx et al., 2014; Narat et al. 2015). Comparison of female behaviors across various differing environments will be important for revealing the evolution of female social relationships and coalitions in bonobos.



Sex combination of dyads

Figure 3-1: Sex combinations and frequency of forming coalition.

Female–female dyads formed coalitions more frequently than did male–female or male–male dyads. The frequency of coalition formation of each dyad was calculated as the (number of coalition A and B both attended in the same side) divided by the (number of aggressions A attended) + (number of aggressions B attended) – (number of aggressions A and B both attended)



Figure 3-2: Affiliative relationships and the frequency of forming female–female coalitions. Each dot represents one female–female dyad.

- a. Same-party attendance index and frequency of coalition formation of dyads
- b. Proximity index and frequency of coalition formation of dyads
- c. Grooming index and frequency of coalition formation of dyads
- d. GG-rubbing index and frequency of coalition formation of dyad



Figure 3-3: Number of agonistic supports (giving and receiving)

Each dot represents an independent female. There was a weak (r = 0.38) but significantly negative correlation between support given and received.



Figure 3-4: Females' winning rate against males in each age category (mean±SE).

Bar with dot is the winning rate of females in dyadic aggressions. Bar with a diagonal

line represents the winning rate of females when they formed a coalition.

Name	Corr	Estimated age		Dependent offspring
(abbreviation)	Sex	in 2012	Age class	(year of birth)
Bokuta (Bk)	Female	49	Old	-
Kabo (Kb)	Female	39	Old	ಧ(2006), ೆ(2012)
Hide (Hd)	Female	35	Old	଼≎(2006), ି(2011)
Maluta (Mt)	Female	27	Middle	ổ(2006), ♀(2012)
Pao (Po)	Female	21	Middle	♀(2009), ♀(2013)
Ichi (Ic)	Female	21	Middle	♀(2007), ♂(2012), ♀(2015)
Saku (Sk)	Female	17	Young	♀(2009), ♀(2013)
Marie (Mr)	Female	12	Young	우(2014)
Nara (Nr)	Female	11	Young	우(2014)
Gai (GI)	Male	39	Old	
Malusu (ML)	Male	30	Middle	
Snare (SN)	Male	21	Middle	
Turkey (TK)	Male	20	Middle	
Daniel (DN)	Male	17	Young	
Ikura (IR)	Male	8	Young	

Table 3-1: Study subjects, estimated age, age category, and their dependent offspring

Predictor variables		Estimates	SE	Z	р
Model 1	Intercept	-3.73	0.36	-10.28	< 0.01
	Sex female-male dyads	-1.82	0.44	-4.14	< 0.01
	male-male dyads	-1.72	0.60	-2.86	< 0.01
Model 2	Intercept	-0.69	1.23	-5.6	< 0.01
	Same-party attendance index	6.31	2.07	3.05	< 0.01
Model 3	Intercept	-3.31	0.32	-10.26	< 0.01
	Proximity index	0.47	1.44	0.32	0.75
Model 4	Intercept	-3.31	0.31	-10.63	< 0.01
	Grooming index	0.42	1.13	0.37	0.71
Model 5	Intercept GG-rubbing index	-3.48 2.50	0.37 2.94	-9.41 0.84	<0.01 0.40

Table 3-2. Results of GLMMs.

The frequency of forming coalitions of the dyads in relation to sex combination of the dyads (Model 1), same-party attendance index of the female dyads (Model 2), proximity index of the female dyads (Model 3), grooming index of the female dyad (Model 4), and GG-rubbing index of the female dyads. Overall, both Model 1 and Model 2 were statistically significant (p < 0.01).

		Recipient of support								
Estimated age in 2012	Supporter	Bk	Kb	Hd	Mt	Ро	Ic	Sk	Mr	Nr
49	Bk		0	2	0	1	4	1	0	0
39	Kb	0		0	1	2	6	0	1	0
35	Hd	1	0		1	2	2	7	3	0
27	Mt	0	0	0		0	1	0	1	1
21	Ро	0	0	0	1		3	5	0	1
21	Ic	0	0	0	0	0		3	0	0
17	Sk	1	0	0	0	0	0		2	0
12	Mr	0	0	0	0	0	1	0		0
11	Nr	0	0	0	0	0	0	0	0	

Table 3-3. Matrix of agonistic support.

The first column gives the estimated age of each female.

A go gotogowiog	Direction of supports					
Age categories	Older support younger	Younger support older				
Old-middle	19	0				
Old-young	12	1				
Middle-young	11	1				
Sum	42	2				

Table 3-4. The direction of support given across age categories.

Chapter 4

Old and dominant females initiate collective departures in wild bonobos in Wamba

1 Abstract

Group-living animals need to coordinate their activity to maintain gregariousness. Although each individual has their own nutritional needs and social and reproductive strategy, they have to reach consensus to decide where and when to travel. Collective movements are considered to be the outcome of one individual's departure followed by other group members. I investigated the initiation of departure of a group of bonobos at Wamba, DR Congo to determine the distribution of leadership between group members. If three or more bonobos started moving more than 30m, we determined the individual who moved first initiating the movement. 256 departures were observed. First, I examined whether the frequency of initiation is different according to the attribute of individuals; sex, age categories, estrous states, dominance, and affiliative relationship. I also examined whether one or some individual(s) initiate departure more or less frequently than expected by chance. Old females initiated departures more frequently than other age and sex categories. Females initiated departures more frequently when they were estrous than when they didn't. Three females initiated more often, and four females and three males initiated less often than expected. All individuals who initiated more often than expected were categorized as old females. This result may be influenced by their dominance structure which old females possess the highest social status in the study group. This pattern of initiation may suggest that the leadership in bonobos is not equally distributed among group members, and old, dominant females are "key individuals" to keep their cohesiveness.

2 Introduction

Group living has advantages, such as reducing predation risk, increasing feeding efficiency, and collectively protecting valuable resources (Nunn 2000; Fashing 2001; Childress & Lung 2003; Majolo et al. 2008). Individuals need to synchronize their activities and maintain cohesiveness to benefit from these advantages, despite the nutritional, social, and reproductive needs of the individual (King & Sueur 2011; Sueur et al. 2013). In particular, when the group travels from one location to another, its members must coordinate when and where to travel, otherwise they might spread apart (King & Sueur 2011). Some individuals might have to shorten their resting time when other individuals start travelling, whereas others might have to wait until some individuals finish feeding before departing.

The process of decision making during collective movement has gained much attention over the past several decades and has been described in various animal species, including species of insects, fish, birds, and mammals (Conradt & Roper 2005, 2007; Petit & Bon 2010). When individuals form a large group, such as a flock of birds or a school of fish, each individual follows one or more simple rules, such as adjusting his/her direction and speed to that of neighboring individuals to synchronize movement and maintain cohesiveness (self-organizing system: Couzin & Krause 2003; Sumpter 2006). On the other hand, in species that form a stable and cohesive social group, wherein group members are able to communicate before or during travel, another rule might maintain cohesiveness, which is that one individual leads group movement while others follow; this is the concept of "leadership" (Pyritz et al. 2011).

When all group members initiate or walk in the leading position equally, the decision-making style is called "equally distributed leadership" (Pyritz et al. 2011). In tonkean macaques (Macaca tonkeana), all individuals, including immature ones, initiate departure at the same frequency (Sueur and Petit 2008, Bourjade & Sueur 2010). At the other extreme of decision-making styles is "personal leadership" (Pyritz et al. 2011), in which one individual constantly leads the group's movement. For example, in the mountain gorilla (Gorilla beringei beringei) the most dominant silverback initiates group movements (Schaller 1963; Watts 2000). However, both the equally distributed and personal leadership styles are rarely observed (Smith et al. 2015). The "partially distributed leadership" style is intermediate to the two extremes, and is most commonly observed among mammals (Pyritz et al. 2011; Smith et al. 2015). In this style, leadership is distributed among group members, but is skewed. Some individuals, who have particular attributes, are more often observed to initiate group departures or to walk in the front position during the travel (King 2010; Smith et al. 2015).

Individuals with high nutrition needs may lead the group's movement because of their relatively high motivation to find food at their next destination (Boinski 1991; Fischhoff et al. 2007; Sueur et al. 2013). Females typically require more energy than males for reproduction, and this might lead to female leadership in some species (e.g., Boinski 1991; Erhart & Overdorff 1999; Fischhoff et al. 2007; Barellich et al. 2008). Moreover, pregnant or lactating females are more likely to travel in front of the group than others in plains zebra (*Equus quagga*), possibly because these females have markedly high nutritional needs (Fischhoff et al. 2007; also see Furrer et al. 2012), although some studies failed to detect similar results (Stueckle & Zinner 2007; Barelli et al. 2008; Belle et al. 2013). In addition, females who display signals of estrus attract males (Nunn, 1999), and may be followed by them.

Experience is also an important factor (King et al. 2009). In an experimental study using homing pigeons (*Columba livia domestica*), individuals who had more experience flying the route led the flock more frequently than did less experienced individuals (Flack et al. 2012; but see also Flack et al. 2013). Also, McComb et al. (2011) found that groups of African elephants which were led by older matriarchs were able to make better decisions when faced with dangerous situations. From this perspective, older individuals might have more knowledge of their range and might be better equipped to lead group members to better feeding or safer resting place (McComb et al. 2001, 2011; Brent et al. 2015).

Social relationships in the group, both agonistic and affiliative, affect the distribution of leadership (King et al. 2009). In species with an apparent dominance hierarchy and intolerant social relationships, higher-ranking individuals often lead group movement (e.g., Squires & Daws 1975; Peterson et al. 2002; Sueur & Petit 2008; King et al. 2009; Nagy et al. 2010; Bonanni et al. 2010). Alternatively, leadership is more likely to be distributed equally in species with no apparent dominance hierarchy and tolerant social relationships (Squires & Daws 1975; Sueur & Petit 2008; Fernández et al. 2013). In species that engage in affiliative interactions, such as grooming and greeting other group members, individuals with strong social affiliations tend to be followed (King, Johnson, & Vugt 2009, King et al. 2008). For example in Tibetan macaques (Macaca thibetana), individuals with higher eigenvector centrality in the proximity network, and individuals who spent more time grooming, successfully initiated departures more frequently than did asocial individuals (Wang et al. 2016).

Most studies on leadership of group movement have been conducted with species which form a cohesive group in which all group members spend time together (Sueur et al. 2011). In species that have a fission-fusion grouping pattern, each individual coordinates the costs and benefits of association with others, and when they do not reach consensus, groups split apart (Kerth et al. 2006). Because the membership of subgroups varies from time to time, it is probable that leadership by a specific individual(s) is unlikely (Fischhoff et al. 2007). Although recent empirical studies have revealed that species living in a fission-fusion society can also exhibit consistent leadership when individuals form strong social bonds (bottlenose dolphins; Lewis et al. 2011, spotted hyena; Smith et al. 2015), information on leadership patterns in fission-fusion societies is still scarce.

Bonobos (*Pan paniscus*) are one of the closest living relatives, evolutionarily, of humans, and live in male-philopatric, multi-male/multi-female social groups of stable membership (Kano 1982, 1992; Eriksson et al. 2006; Sakamaki et al. 2015). They mainly feed on ripe fruit (Kano & Mulavwa 1984; White 1998) and have a fission-fusion association pattern in which a group splits into temporary subgroups ("parties"; Kano, 1982). Although bonobos were reputed to be egalitarian (de Waal 1997), empirical studies have shown that their dominance style is not as egalitarian as previously considered, being rather a despotic dominance hierarchy (Vervaecke et al. 2000; Paoli et al. 2006, Stevens et al. 2005, Surbeck & Hohmann 2013, this study). On the other hand, researchers agree that they are highly tolerant (defined as dominants and subordinates with close
relationships, low levels of violence, frequent reconciliation, and high levels of tolerance around contested resources) of each other, especially among females (Kano 1992; Parish 1994; Furuichi 1997; Vervaecke et al. 2000; Palagi et al. 2004; Hare et al. 2007; Stevens et al. 2005; Yamamoto 2015; Chapter 3).

Kin-selection theory predicts that males should be more gregarious and cooperative than females in male-philopatric societies (West-Eberhard 1975; Silk 2002). Despite this, female-female pairs of bonobos associate as frequent as, if not more than, male-male or male-female pairs (Kuroda 1979; White 1988, 1998; Kano 1992; Furuichi 2009, 2011; Hohmann & Fruth 2002). Females aggregate in the central part of the party, and seem to play an important role in decisions regarding group movement. Furuichi (2011) argued that female bonobos initiate party movement and described the departure process of wild bonobos as follows: "Party movements typically occur when members descend from a tall fruit tree and take a short break on lower trees, observing one another. Some of the males climb down and perform branch-dragging behavior while running on the ground, seemingly to propose a direction of movement. However, the entire party does not move until the dominant females climb down and initiate movement in a direction of their own choice." (Furuichi 2011, pp132-133) However, this observation was not tested by systematic study.

The goal of this study was to examine the distribution of leadership styles in wild bonobos. In this study, I focused on determining the factors affecting the timing and direction of departure (i.e. initiation; Pryitz 2011) during group movement, although individuals who initiate departure and who walk in the leading position are not necessarily same (Pryitz 2011). I used two approaches; attribute-based analysis and individual-based analysis. First, I examined whether the frequency of initiation was different according to the attribute of individuals: sex, age categories, estrous states, dominance, and affiliative relationships. I did not assess the reproductive status of females. Because their reproductive cycle, wherein they come into estrous during pregnancy and lactation (Furuichi 1987), made it difficult to determine the status (pregnancy, lactating, or cycling) of each female. Using the individual-based analysis, I examined whether one or more individual(s) initiated departure more or less frequently than expected by chance.

Because animals with high nutritional needs may determine the timing of departure, I predicted that females initiated departures more frequently than males, especially estrous females that attract adult males, which follow them. Because the lead by individuals who possess greater social knowledge may give benefits to followers, older individuals might initiate departures more frequently than younger individuals. Because of their tolerant social relationships, I predicted that dominance does not affect the frequency of initiation, and none of the group members would initiate departures more or less frequently than expected. Finally, I predicted that individuals with a higher eigenvector value of centrality in grooming networks would initiate departures more often than individuals with smaller eigenvector values of centrality because of their affiliative relationships in the group.

3 Methods

3-1 Study site and Subjects

Observations were conducted on the PE group of wild bonobos in the Wamba, Luo Scientific Reserve, Democratic Republic of the Congo, where long-term research has been conducted since 1974 (Kano 1992). From 1976, researchers were aware of the presence of bonobos in the PE group's current range, and at the time they named them the "P group" (Kuroda 1979; Kano 1982; Idani 1990). Research at Wamba was disrupted in 1996 because of political instability and re-initiated in 2003 with continuous daily observations of P group's neighbor, the E1 group. In September 2010, we began a habituation procedure and following a group in the old P group range daily, but because we could not immediately confirm whether it was the same group, we named them the "PE group." After identifying individuals in PE group, we examined old photographs of the P group taken before 1991 and found that two parous females, Yuba and Ruri, from the P group (Idani 1990) were present in the PE group, and had been renamed Bokuta and Kabo (Table 4-1), respectively. The PE group is therefore likely to be the same as the P group that was studied pre-1996.

The PE group consisted of 26–27 individuals. All individuals were identified and habituated from the beginning of the study period. Our study subjects were mature individuals greater than 8 years old, excluding one female who emigrated during the study period (15 individuals: 9 females and 6 males, Table 4-1). Data from females who temporary visited this group were not analyzed. I estimated the age of subject animals based on their physical features. Individuals estimated to be 35 years old or older were classified as old, and individuals from 21 to 34 years old were classified as middle-aged. Individuals estimated to be 20 years old or less were classified as young. The kin relationships of the study subjects were not known, except for a middle-aged female, Ichi, the known mother of the young male Ikura.

3-2 Behavioral observation

Parties of bonobos were observed for 1698 hours with the help of two local assistants, from August to November, 2012; August, 2013 to January, 2014; July to September, 2014; and January to June, 2015. The general activity that most of the party members were engaging in was continuously recorded (i.e., resting, feeding, and travelling). I recorded all observed intra-group aggressive interactions to assess the dominance relationships. I also recorded grooming interactions by instantaneous scan sampling (Altmann 1974) for all visible individuals. I recorded whether they were grooming any other individuals at 5-min intervals. The firmness of each female's sexual swelling was scored on a daily basis (see Ryu, Hill & Furuichi, 2015 for the detail).

Collective departures were defined as occurring when at least three of the subject individuals moved in the same direction more than 30 m horizontally, regardless of moving on ground or arboreal, without stopping after engaging in an activity other than traveling for a period of at least 5 min. For each departure, the individual who started moving first was defined as an initiator, who determined the timing and direction of the departure. I recorded the identity of the initiator and other subject individuals following the initiator. Each follower had to join the departure within 1 min after the previous follower moved. These parameters were defined during a pilot study conducted 2 months prior to this study period (Pyritz et al. 2010; Pyritz et al. 2011). For this study, I used the departures in which the initiator-followers relationship was clear. For example, when two animals started moving simultaneously and other individuals joined the movement, I discarded the data because I could not determine who was the initiator. I calculated the frequency of being an initiator ("Initiation Index") for each individual. The "Initiation Index" of an individual (A) was calculated as follow:

Initiation Index (A) = the number of departures that (A) initiated / the number of departures that (A) participated in.

In this study, I analyzed only the initiation-following relationships of successful group departures by three or more individuals. I refrained from recording the cases in which one or two individuals left, because such individuals often leave the party quietly and it is difficult to observe them in the dense vegetation. Branch dragging of males was considered to be a pre-departure behavior in bonobos (Ingmanson 1996), but was not analyzed in this study because branch dragging was also used as a displaying behavior by males (Kano 1992). Consequently, it was difficult to distinguish between these two forms of the behavior.

I calculated the score of each individual's affiliative relationships using the eigenvector of centrality in the grooming network (Sueur et al. 2011). I collected $5,403 \pm 1,491$ scan samples per subject individual (average \pm SD). I calculated the grooming index for each pair of individuals to construct a grooming matrix. The grooming index was calculated as follows: the number of scans during which a pair was observed grooming divided by the number of scans during which the pair was detected. I calculated the eigenvector centrality coefficient for each individual using UCINET software (Table 4-

1).

3-3 Data analysis

All statistics were conducted using R version 3.2.3.

The attribute-based analysis

I ran GL(M)Ms to examine the effects of each individual's physiological and social factors on the initiation index. In each model, Initiation indices for each individual were used as a predictor using the "c-bind" function and binomial error distribution. The level of significance was set at 5%. Probabilities between 5% and 10% are reported as trends.

I ran a generalized linear model (GLM) to examine the effect of age and sex on the initiation index. I used age, sex, and interaction of age and sex as fixed factors.

The effect of dominance status on the initiation index was examined only in males because dominance status in females largely correlated with their age; older females were more high-ranking than younger ones (Furuichi 1989, 1997; Vervaecke et al. 2000; Chapter 3). The male dominance hierarchy was determined using the outcome of dyadic male-male aggression. From June 2012 to March 2015, the dominance hierarchy among males was stable and the alpha-male was SN. However, after multiple individuals severely attacked SN on March 5, 2015, his dominance status dropped to the rank of 3rd or 4th (N. Tokuyama, personal observation). Because of this drastic change in their dominance hierarchy, I used data of both initiation of departures and agonistic interactions, which were observed before March 4, 2015, to examine whether dominance status affected the initiation index for males. The dominance rank between June 2012 and March 4, 2015 was significantly liner (h' = 1, p = 0.023). I used the initiation index of each male as the predictor, with their age category and rank as fixed factors.

To examine whether a female's estrous state affected her initiation index, I ran a generalized linear mixed model (GLMM) (package "lme4"). I calculated two initiation indices for each female—when they had maximal sexual swelling and when they did not.

I used the initiation index as the predictor, with the age category and swelling state as fixed factors. IDs of females were used as a random factor. Additionally, to determine whether estrous females attracted males, I compared the number of both male and female followers between cases in which the initiator was a female with maximal swelling and cases in which the initiator was a female with non-maximal swelling using the Wilcoxon rank-sum test.

To examine whether an individual's centrality in the grooming network affected the initiation index, I conducted a GLM. I assigned the initiation index of each study individual as the predictor, with his or her eigenvector centrality coefficient in the grooming network as a fixed factor. Because grooming interactions of individuals were not independent of their sex or age (Hohmann et al. 1999, Stevens et al. 2006), I also used sex, age, and interaction of sex and age as predictors.

Individual-based analysis

To determine whether specific individual(s) initiated departures more or less than expected, I compared the number of times each individual initiated a departure to the number expected based on 1,000 randomization iterations for each individual (randomization protocol: Manly 2006; see also Lewis et al. 2011). For all departures in which an individual participated, I randomized the order of individuals and counted the number of departures in which the individual was in the first position. I repeated this procedure 1,000 times for each individual. I compared the observed number to the distribution of expected number of departures for which the individual was the initiator. I considered an individual initiated departures more than expected if the observed number was greater than 97.5% of the randomization distribution, and less than expected if the observed number was less than 2.5% (p < 0.05 for a two-tailed test).

4 Results

Party contained 9.8 ± 3.2 subject individuals on average (6.0 females and 3.8 males) during the observation period. I observed 256 successful departures. Departure contained 6.1 ± 2.6 subject individuals on average (4.1 females and 2.0 males). All subject individuals were observed to initiate departures at least once.

4-1 Sex and age of the individual

I found that older individuals had a higher initiation index, and sex did not significantly affect that the initiation index. However, I found an effect of interaction between age and

sex (GLM, Table 4-2 (a)). This interaction indicated that the effect of sex was detected in the old age category (Figure 4-1).

4-2 Estrous states and age among females

Among females, both their age categories and estrous status affected the initiation index. Older females initiated departures more frequently than did younger females, and females initiated departures more frequently when they were in estrus then when they were not (GLMM, Table 4-2 (b), Figure 4-2). Neither the number of male followers nor female followers significantly increased when the initiator was estrous (non-estrous female initiator (n = 114) vs. estrous female initiator (n = 94): 1.88 male followers vs. 1.93 male followers, Wilcoxon rank sum test, W = 5,783, p = 0.31; 4.16 female followers vs. 4.23 female followers, Wilcoxon rank sum test, W = 5,699, p = 0.49).

4-3 Social rank and age among males

Among males, dominant males tended to have a higher initiation index than subordinate males (GLM, Table 4-2 (c), Figure 4-3). The age categories were not significantly related to the initiation index (GLM, Table 4-2 (c)).

4-4 Sociality of individuals

There was a trend for the values of the eigenvector centrality coefficients in the grooming network to be negatively correlated with the initiation index (GLM, Table 4-2 (d), Figure 4-4).

4-5 Individual-basis differences on initiation

Three females (Kb, Bk, and Hd) initiated departures more frequently, and 3 males (ML, GI, and IR) and 4 females (Mt, Sk, Mr, and Nr) did so less frequently than expected by chance (Figure 4-5). All three who initiated departures more frequently than expected were old females.

5 Discussion

I examined the initiation of departures in wild bonobos, which have a fission-fusion grouping pattern and are known to be one of the most tolerant species among non-human primates. Species with high levels of social tolerance tend to have an equally distributed leadership (Conradt & Roper 2005; Sueur & Petit 2008; Pyritz et al. 2011). I found that all individuals initiated departures at least once, but the frequency of initiation was greatly skewed based on their attributes, suggesting that wild bonobos in this study exhibited a rather strong "partially distributed leadership" (Pyritz et al. 2011b).

Although females coordinated group movements more frequently than males in many social mammals (e.g., Fischhoff et al. 2007; Barelli et al. 2008; Belle et al. 2013), I did not find a significant sex difference in the initiation index in this study of bonobos. Instead, I found a significant interaction between sex and old age, which indicated that the effect of sex was detected in the old age category. Among middle-aged and young individuals, females and males initiated departures almost equally. Only among old individuals did females initiate departures significantly more frequently than males. This result might be attributed to two factors: experience and social dominance.

I found that older females initiated departures more often than did younger females. Initiation by aged individuals was observed in African elephants (*Loxodonta africana*; McComb et al. 2001), giant otters (*Pteronura brasiliensis*; Davenport 2010), giraffes (*Giraffa camelopardalis*; Berry & Bercovitch 2014) and killer whales (*Orcinus orca*; Brent et al. 2015). This pattern might occur because aged individuals have more experience and knowledge of their range (King & Sueur 2011). In killer whales, females live more than 30 years after menopause, and these females tend to be in the lead position during group movement (Brent et al. 2015). In food-scarce years, post-menopausal females are in the lead position more often than during food-abundant years, suggesting their level of experience is why older females lead the group more than younger individuals (Brent et al. 2015). Bonobos mainly feed on ripe fruit (Kano & Mulavwa 1984, Kano 1992; White 1998). Fruiting trees are widely dispersed throughout their range, and the abundance of fruit for a species varies among seasons and years (Mulavwa et al. 2008, Terada et al. 2015). Janmaat et al. (2013) showed that chimpanzees (P. troglodytes) use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons (see also Janmaat et al. 2006 for similar results in wild sooty mangabeys (Cercocebus atys atys] and grey-cheeked mangabeys (Lophocebus albigena)). It may be possible that younger individuals follow older individuals because they possess more experience about fruiting patterns in their range. However, this tendency was not detected among males, who should have more experience in their range than females of the same age because males stay in their natal group for life, whereas females immigrate into the group when they are approximately 10 years old (Kano 1992, Eriksson et al. 2006; Sakamaki et al. 2015).

Although it was not significant, I found a trend for dominant males to have higher initiation indices then other males. I did not assess the effect of dominance among females because dominance rank was strongly correlated with age (Furuichi 1989, 1997; Vervaecke et al. 2000; Chapter 3). Considering that older females initiated departures more frequently than younger females, it could also be concluded that dominant females initiated departures more frequently than subordinate females. In all captive and wild bonobo groups, some females clearly possess higher social rank than males (Furuichi 1997, 2011, Vervaecke et al. 2000, Surbeck & Hohmann 2013). I could not determine a linear dominance hierarchy containing both males and females in this study because the number and combinations of dyadic inter-sex aggressions were too few. However, during this study period, old females won 84% of inter-sex dyadic agonistic interactions, whereas middle-aged and young females won 69% and 29% (Chapter 3) of their interactions, respectively, suggesting that old females were apparently dominant over males. The dominance structure of bonobos in this group may have attributed to our finding that old females initiated departures more often than other age and sex categories.

Prolonged estrous periods are an important aspect in bonobos (Furuichi 1987; Kano 1992). Although female chimpanzees exhibit maximal sexual swelling only when they are fertile, female bonobos do so even during non-ovulatory periods (Reichert et al. 2007). In our study, females initiated departures more frequently when they exhibited maximal swelling than when they did not. This might reflect the fact that males were attracted to estrous females as mating partners, and as such followed them. However, the number of both male and female followers did not significantly increase when the initiator was an estrous female, compared to when the initiator was a non-estrous female. This suggested that estrous females did not particularly attract males or females. This result corroborates the findings of Ryu et al. (2015), who showed that estrous females attracted not only males but also females, and frequently engaged in affiliative interactions. I did not collect data on the following order of individuals during departure events, and I am unable to determine whether estrous females attracted males first, with other females simply following them to maintain group cohesiveness, or whether estrous females attracted both males and females simultaneously. Although further study is needed to understand why these females were more likely to initiate departures, a benefit of the prolonged estrus period in female bonobos might be that it enables them to decide when to depart.

The eigenvector centrality coefficient in grooming networks was not significantly correlated with the initiation index. In most studies which reported the effect of affiliative relationships on leadership distribution, a strong effect of other attributes, such as social dominance, was not found (Sueur & Petit 2008; Ramseyer 2009; Wang et al. 2016). The strong effect of dominance and age may have masked or exceeded that of affiliative relationships in this study. It is worth noting that the oldest female, Bk, who had the highest initiation index in the group, had the lowest eigenvector centrality coefficient value in the grooming network.

The gregariousness of females is strikingly different between female bonobos and female chimpanzees. Despite living in a male-philopatric society, female bonobos are more cohesive and centralized in the party than males (Kuroda 1979; White 1988, 1998; Kano 1992; Furuichi 2009, 2011; Hohmann & Fruth 2002). Although there is interpopulation variation (Lethmann & Boesch 2008), the gregariousness in female chimpanzees is generally weak. The difference in female gregariousness between the two species is not satisfactorily explained by ecological factors, such as food abundance (Furuichi 2009, Clay et al. 2015).

In Chapter 3, I found that female coalitions might be developed as a counterstrategy against male harassment, and the increased importance of forming coalitions might actually enhance female gregariousness in bonobos. The coalitions were formed by a uni-directional relationship, in which older females supported younger females, making associations with older females potentially very beneficial for younger

ones (Chapter 3). In this study, both the attributed-based analysis and the individual-based analysis suggested that old (and dominant) females might be the key individuals for maintaining party association, corroborating the results of Chapter 3. The gregariousness of female bonobos may be maintained by the motivation of younger, subordinate females to follow older, dominant females.

Three females initiated departures more than expected in the individual-based analysis, suggesting that these individuals were habitual initiators in this group. The leadership by a restricted set of individuals is considered less likely in a fission-fusion society (Fischhoff et al. 2007). However, recent studies, including this study, are revealing that the relationship of habitual leaders and followers does emerge in fissionfusion societies. Lewis et al. (2011) found that some individuals consistently acted as leaders of group movement in bottlenose dolphins (Tursiops truncatus), another dynamic fission-fusion grouping species. The dolphins encountered abundant food resources more frequently when they were led by habitual leaders than when they were led by other individuals (Lewis et al. 2013). The spotted hyena (Crocuta crocuta) also exhibits a flexible fission-fusion society, and individuals follow the movement of the most dominant female in the subgroup (Smith et al. 2015). Individuals are motivated to associate with a specific individual(s), for example, to gain from experienced individuals (Lewis et al.

2013) or to obtain protection or mating opportunities (this study). Leadership by such an individual(s) might occur more readily in fission-fusion species than in species in which strong group cohesiveness occurs because subgroups may not meet for several hours, days, or weeks (Aureli et al., 2008).

Although equally distributed leadership has the lowest consensus cost to group members (Conradt & Roper 2003), it seems the distribution of individuals in leadership roles is skewed in all group-living great apes. Although there is no systematic study, mountain gorillas are reported to have personal leadership, wherein the dominant silverback leads group movements (Schaller 1963; Watts 2000), and dominant male chimpanzees coordinate group movement (Boesh & Boesh-Achermann 2000). In bonobos, I found that the leadership of group departures was partially distributed and the old and dominant females most frequently dictate the timing of departures. Feeding habits and social organization varies among subspecies of gorillas (Yamagiwa et al. 2003). Patterns of fission-fusion dynamics, strength of social bonds, and dominance steepness are different between groups of chimpanzees and bonobos (Boesch et al. 2002; Lehmann & Boesch 2008; Kaburu & Newton-fisher 2015). A comparison of the leadership distribution among groups of great apes with different social patterns might give us

important insights for understanding the emergence and evolution of various types of leadership roles in humans.



Figure 4-1: The effect of age and sex on the initiation index (mean±SE).

Bar with a diagonal line represents the Initiation Index of females. White bar represents the Initiation Index of males. There was a significant effect of interaction between age and sex, indicating that the effect of sex was detected in the old age category.



Figure 4-2: The effect of age and estrous stats on the initiation index among females (mean±SE).

Bar with a diagonal line represents the Initiation Index of estrous females. White bar represents the Initiation Index of non-estrous females.



Figure 4-3: Male's dominance rank and Initiation Index

Although it was not significant, there was a trend that dominant males have a higher initiation index than subordinate males.



Figure 4-4: The relationship between Initiation Index and the individual's centrality in the grooming network

There was a trend that individuals with higher values of the eigenvector centrality coefficients in the grooming network had lower Initiation Index.



Figure 4-5: The Initiation Index of each individuals. One asterisk means that the individual initiated departures more frequently than expected. Two asterisks arranged in tandem mean that the individual initiated departures less frequently than expected. Black, grey and white color represent that the individual is old, middle, and young age, respectively.

ID	Sex	Estimated	Age class	Dependent offspring	Dominance rank	Eigenvector centrality coefficient
(abbreviation)		age in 2012		(born year)		in grooming network
Bokuta (Bk)	Female	49	Old	-		0.056
Kabo (Kb)	Female	39	Old	੍ਰ(2006), ੈ(2012)		0.26
Hide (Hd)	Female	35	Old	ੈ(2011)		0.24
Maluta (Mt)	Female	27	Middle	്(2006), ♀(2012)		0.41
Pao (Po)	Female	21	Middle	♀(2009), ♀(2013)		0.26
Ichi (Ic)	Female	21	Middle	♀(2007), ♂(2012), ♀(2015)		0.37
Saku (Sk)	Female	16	Young	♀(2009), ♀(2013)		0.10
Marie (Mr)	Female	12	Young	우(2014) 우(2014)		0.24
Nara (Nr)	Female	11	Young	Ç(2014)		0.24
Gai (GI)	Male	39	Old		5	0.20
Malusu (ML)	Male	30	Middle		3	0.23
Turkey (TK)	Male	21	Middle		2	0.33
Snare (SN)	Male	20	Middle		1	0.31
Daniel (DN)	Male	17	Young		4	0.21
Ikura (IR)	Male	8	Young		6	0.15

Table 4-1: Study subjects, estimated age, age category, their dependent offspring, social dominance, and value of eigenvector centrality

coefficient in the grooming network.

(a)	Estimates	SE	Z	р
Intercept	-2.08	0.16	-12.91	< 0.01
Age - old	1.09	0.19	5.86	< 0.01
Young	-1.43	0.39	-3.36	< 0.01
Sex – male	-0.12	0.24	-0.52	0.60
Sex-male: Age-old	-1.29	0.50	-2.60	< 0.01
Sex-male: Age-young	0.47	0.63	0.74	0.46

(b)	Estimates	SE	Z	р
Intercept	-1.72	0.28	-5.96	< 0.01
Estrous states				
- estrous	0.52	0.18	-2.87	< 0.01
Age - old	1.53	0.35	4.30	< 0.01
- young	-1.44	0.50	-2.91	< 0.01
(c)	Estimates	SE	Z	р
Intercept	0.18	0.02	8.62	0.013
Dominance rank	-0.52	0.31	-1.70	0.090
Age - old	1.01	0.99	0.99 1.03	
- young	1.42	1.26	1.12	0.26
(d)	Estimates	SE	Ζ	р
Intercept	-1.57	0.35	-4.55	< 0.01
Eigenvector centrality of grooming network	-1.56	0.93	-1.67	0.093
Age - old	0.89	0.22	4.00	< 0.01
- young	-1.64	0.41	-3.98	< 0.01
Sex – male	-0.18	0.24	-0.74	0.45
Sex-male: Age-old	-1.24	0.50	-2.42	0.013
Sex-male: Age-young	0.52	0.63	0.83	0.41

Table 4-2: The result of GL(M)M.

- (a) The effect of age and sex on the Initiation Index.
- (b) The effect of age and estrous states on the Initiation Index among females.
- (c) The effect of male's dominance rank on the Initiation Index.
- (d) The effect of the value of eigenvector coefficient centrality in the grooming network on the Initiation Index.
- Overall, model (a), (b), and (d) were statistically significant (p < 0.01).

Chapter 5

General discussion

1 Summary of results

In Chapter 2, I reported a case study, where bonobos travelled a long distance in the apparent search for a group member, ML, who was caught in a snare in the swamp forest. Four adult animals stayed with ML longer than the others, but ended up abandoning him to join the others for sleeping in a dry part of the forest. The next morning, they split into two parties; one party seemed to travel in a direction to where ML was left and another party that I followed travelled in a different direction. However, when the latter heard voices from the former, the latter changed its course and followed the former to reach the site where ML was left on the previous day. Such examples of decision-making suggested that bonobos, both males and females, have a strong motivation to stay in a large party and to maintain their group cohesion.

In Chapter 3, I examined the role of female coalitions on their gregariousness and affiliative interactions. The results suggested that female coalitions in bonobos might have evolved as a counter-strategy against harassment by males. Females might choose their coalition partners based not on affiliative relationship or reciprocity, but rather on mutualism.

In Chapter 4, I investigated who determines the timing of party departures when the group starts travelling, in order to clarify whether a specific individual(s) has the role of maintaining cohesiveness. I found that old and dominant females initiated travelling departures more frequently than other age-sex class individuals, suggesting that such individuals play a key role in maintaining the cohesiveness of the group.

2 The relationship among female coalition, gregariousness, and affiliative interactions

The cooperation among females against harassment by males might be at the heart of female social relationships in bonobos. Male mammals have been reported to behave aggressively toward females to coerce copulations, acquire higher social status than females, or without any obvious purposes (Clutton-brock & Parker 1995; van Schaik et al. 2004; Muller & Wrangham 2009). Females incur a substantial cost due to male aggressiveness, which causes elevated cortisol levels in females (Muller et al. 2007), increases their energy expenditure (Sundaresan et al. 2007), and often results in serious injuries (Chilvers et al. 2005; Muller et al. 2009). In addition, males sometimes commit infanticide (Sugiyama 1984; Hamai et al. 1992; van Schaik & Jonson 2000). Female

primates have evolved various strategies against such harassment, such as avoiding the company of males (chimpanzees; Otali & Gilchrist 2005), and developing friendly relationships with a particular male (baboons; Palombit 2009). The formation of female coalitions has been considered as one of the key strategies for escaping harassment by males (Smuts & Smuts 1993), even though female coalitions primarily serve to cope with competition among females (Isbell & Vuren 1996; Sterck et al. 1997). The use of coalitions against males has remained anecdotal (reviewed by Smuts & Smuts 1993; Perry 1998; Setchell et al. 2006).

In bonobos, female coalitions have been thought to be useful for preventing harassment (Kano 1992; Parish 1994, 1996; Hohmann & Fruth 2003; White & Wood 2007; Furuichi 2011). Also, it had been considered that females use affiliative interchanging to promote coalition formations (Parish 1996). In Chapter 3, I *did* find that female bonobos form coalitions against harassment by males. Females of all age categories benefited from coalitions, as they could win against males more easily in coalitions than when they confronted a male alone. However, affiliative relations between specific females did not promote coalition building between them, and the females formed coalitions rather opportunistically while staying in the same party. Thus, not the affiliative interactions, but belonging to the same party might be important for female coalition

formation. In a fission-fusion social system, chimpanzee females might avoid to stay in a large party to receive less aggressions from males (Otali & Gilchrist 2005). In contrast, bonobo females might have evolved female-female aggregation and cooperation to escape harassment by males.

As explained above, being gregarious might be beneficial for female bonobos. However, the more females aggregate, the higher is the competition among them (van Shaik 1996). If access to resources is greatly biased toward some individuals, other individuals might avoid associating with them in a fission-fusion social system (Aureli et al. 2008). For example, in chimpanzees, feeding competition among females is an important determinant of their association patterns (Muller 2008; Williams et al. 2008). Affiliative interactions might be exchanged in return for tolerance, for example, grooming is exchanged for tolerance during feeding in several primate species (Kapsalis & Berman 1996; Ventura et al. 2006; Carne et al. 2011; Tiddi wt al. 2011). GG-rubbing occurs most commonly during feeding and may reduce tension, allowing females in a group to cofeed (Kuroda 1980; Furuichi 1989; Parish 1994; Hohmann & Fruth 2000; Ryu et al. 2015). As the importance of female aggregation increased, frequent affiliative interactions among females might have developed to enhance tolerance, and mitigate inequality in resource consumption.

When tolerance among females increases, owing to frequent affiliative interactions, females are able to aggregate more easily, leading to a high frequency of coalition formation. Coalitions may decrease the cost of aggregation for females, for example, by acquiring feeding priority over males (White & Wood 2007), making it easier for females to aggregate. The strong female social bonding in societies with high female-dispersal might have been established and reinforced by these positive feedbacks.

3 The mechanism of age-ordered centrality of female gregariousness

Although coalition formation is beneficial for all females, the benefits might be greater for young females than for old ones. Old females seemed to enjoy a higher social status than males, and were able to win against males by themselves. Younger females were less likely to win against males in dyadic aggression than were old females. In addition, there was a unidirectional relationship between females, such that older females supported younger females. Therefore, staying with older females was potentially very beneficial for the younger ones. The gregariousness of female bonobos might be maintained by the tendency of younger females to follow older females, i.e., the motivation for females who need protection to follow the females who provide it.

Chapter 4 showed that older females initiated group departures and the younger

females followed them. This result *did* confirm that older females attract younger females. By deciding the timing and direction of group travelling, older females might be able to enjoy the benefits of group living with minimized consensus cost (Conradt & Roper 2003, 2005). Even for old females, attracting other females might be beneficial, as it could enhance the mating success of their sons, who are usually in the same party with them. Male mating success is shown to be higher when they are supported by their mothers (Surbeck et al. 2011). With more females around, a mother might gain indirect reproductive fitness through her sons. Thus old females might actively support younger females, not only because they gain the direct benefit of winning against males, but also because they are able to enhance the benefits of group-living by attracting other females around them.

4 Non-agonistic and age-ordered hierarchy among females in Wamba

The various benefits of association between older and younger females may shape their asymmetrical relationships. Although rare, agonistic behavior is sometimes shown by old females toward younger females, while the younger females rarely show aggressive behavior toward the older ones (Furuichi 1997; Chapter 3). Moreover, the interactions between females within a dyad are generally biased toward the older female; at Wamba, old females receive more grooming than the younger ones (Ryu et al. 2015), food is transferred from older to younger females (Yamamoto 2015; S. Yamamoto, personal communication), and younger females follow the travelling decisions of the older ones (Chapter 4). These interactions are also often correlated with the social hierarchy in other animal species (grooming: Tiddi et al. 2012; food sharing: Stevens & Gilby 2002; initiation: Sueur & Petit 2008; Nagy et al. 2010). Although it is difficult to determine a dominance hierarchy based on the outcome of dyadic aggressions among wild female bonobos (Surbeck & Hohmann 2013; Chapter 3), these consistent patterns of asymmetrical relationships indicate the existence of a clear hierarchy, whereby the old females are dominant over the younger ones.

Generally, animals acquire their dominant status via a series of agonistic interactions (Holekamp & Smale 1991). In addition, dominance should constantly be asserted or reinforced through aggression on the part of dominant individuals (Prud'Homme & Chapais 1993; Forkman & Haskell 2004). In chimpanzees, resident females actively attack immigrant females (Nishida 1989; Kahlenberg et al. 2008). In bonobos as well, aggressive behavior by resident females toward the newly immigrant females is observed (Idani 1991; Sakamaki et al. 2015), which might be instrumental in determining the social status of young females. However, since aggressive interactions among resident females are rarely observed (Furuichi 1997; Surbeck & Hohmann 2013; Chapter 3), it is unlikely that their hierarchy is maintained or reinforced by aggression.

For the females of a gregarious species, acquiring a high social status is beneficial as it can improve their access toward better resources, which could translate into higher reproductive fitness (Stockley & Bro-Jørgensen 2011). In female bonobos, however, inequalities in resource access might be minimized due to high tolerance. As I have discussed above, making associations with older females is potentially very beneficial for younger females, as the older females can protect them from harassment by males. Young, subordinate females might not dare to challenge the older, dominant females, as the potential gain in benefits is low and they risk losing protection. This might help them to shape an age-ordered hierarchy without any apparent aggressive acts.

The situation might be different when females compete for the social status of their sons. In bonobos, mothers support their sons during the rank struggle of males, and sometimes, severe aggression between two mothers is observed (Furuichi 1997, 2011). During my study period, the dominance hierarchy of males was stable (see Methods of Chapter 4), and I hardly observed any challenging behavior among them. However, in the neighboring group E1, challenging behavior among males was frequently observed, especially from 2013 to 2014, accompanied by severe fights involving their mothers,
where the alpha female was attacked and injured by younger subordinate females (Furuichi and other, unpublished observations). Therefore, comparing the patterns of female coalition formation, affiliative interactions, and aggressive interactions between the stable and unstable male dominance period might provide a better understanding of female relationships among bonobos.

5 Inter-sex dominance hierarchy structure in bonobos

In both wild and captive groups of bonobos, some females clearly possess a higher social status than males (Furuichi 1997, 2011, Vervaecke et al. 2000, Surbeck & Hohmann 2013). However, these females might not be 'physically stronger' than the males. As discussed above, young females seem to possess a lower social status than males, and support from the older females might enable them to stay central to the party without suffering from harassment by males. In such a circumstances how do females acquire a higher social status than males as they get older? In Japanese macaques, immature females receive consistent support from their mothers, and become to receive consistent submissive behavior by females of subordinate matrilineage (Kawamura 1958; Chapais 1988). Similarly in bonobos, frequent support by older females might help the younger females to improve their social status against males, and eventually the males might start showing

submissive behavior toward them.

6 Conclusion and further perspectives

This study revealed that strong female social bonding in bonobos might have evolved because being gregarious was beneficial for females to counter harassment by males. In addition, they might have developed frequent affiliative interactions for tolerance, as the inequalities must be minimized for unrelated females to stay together in their fissionfusion society. The protection provided by the old females to younger ones might shape their age-ordered hierarchy and centrality in the party. When females maintain their cohesiveness, males tend to stay with them because their fitness is determined by mating success (van Schaik 1996). As a result, bonobos might have developed their gregarious nature, which would explain the occurrence of the case that I reported in Chapter 2.

For further progress of this study, DNA analysis to understand kin-relationships among the study subjects is necessary. I discussed earlier that older females might support younger females as it might be beneficial to them by enhancing the mating success of their sons. It would be interesting to examine whether the behaviors are different between females with and without adult sons.

A theoretical and modeling approach might be useful to explain the evolution of

female relationships in bonobos. I may consider a model which includes the benefits of providing support, both direct and indirect, in addition to the costs of being gregarious, such as feeding competition. Moreover, the possibility of betrayer, such as a female who attack other females and monopolize resources, and provision for punishment need to be considered. Using these additions, I might be able to conduct simulations to understand the conditions under which sociality in female bonobos could potentially evolve.

In addition, comparison of female sociality across different environments is needed. Most studies of wild bonobos, including mine, have been conducted in dense forest habitats where the food availability is relatively high and stable (White & Wrangham, 1988; White, 1998). However, bonobos live in diverse environments, including the mosaic forest which contains vegetation of both forest and savanna, where conservation, habituation, and research activities have begun quite recently (Inogwabini et al. 2008; Serckx et al. 2014; Narat et al. 2015). Comparison of female behaviors across different environments would be important for understanding the evolution of female gregariousness and social bonding in bonobos.

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