

Chapter 6

Intergroup Transfer of Females and Social Relationships Between Immigrants and Residents in Bonobo (*Pan paniscus*) Societies

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Introduction

Bonobos (*Pan paniscus*) form multi-male and multi-female unit groups (community) that regularly divide into temporary parties (Kuroda 1979; Kano 1982; White 1988). Although such fission–fusion dynamics occur to some extent in the social systems of most other species (Aureli et al. 2008), bonobo societies are unique in their tendency toward bonding among female nonrelatives, scarcity of male bonding despite male residence, and relative absence of males outranking females (Kano 1992; White 1996; Furuichi 2011). This is in striking contrast with another of our closest living relatives, chimpanzees (*Pan troglodytes*); chimpanzee males form a coalition network, females are less social than are males, and female and immature individuals offer submissive greetings to adult males. However, both *Pan* species

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show strong tendencies toward female dispersal and male residence (Nishida 1979; de Waal 1982; Goodall 1986; Wrangham 1986; Nishida and Hiraiwa-Hasegawa 1987; Furuichi 1989; Kano 1992).

Itani (1977, 1985) argued that female or male philopatry is a phylogenetically stable social feature. However, there have been several reports of exceptions to male philopatry and female transfer in chimpanzees and bonobos. In some cases involving chimpanzees at Gombe and Mahale in Tanzania, females remained and gave birth in their natal group (Goodall 1986; Nishida et al. 2003). Both male and female chimpanzees seemed to emigrate from their natal group at Bossou in Guinea (Sugiyama 1999, 2004), although the emigration of those animals to other unit groups has not been confirmed. Possible male immigration was reported in a bonobo society at Lomako in the Democratic Republic of the Congo (DRC; Hohmann 2001). Immigration of adult males and adult females with offspring, which was considered a result of a group fusion, was observed in a bonobo group at Wamba in DRC (Hashimoto et al. 2008; Furuichi et al. 2012; see below for details). It is important to understand the circumstances under which such exceptional cases occur when examining the evolutionary models used to explain sex-biased dispersal patterns.

Sex-biased dispersal is an almost ubiquitous feature of the life history of mammals, and many articles have attempted to explain the diversity of sex-biased dispersal patterns (Handley and Perrin 2007), such as the avoidance of inbreeding (Itani 1972; Pusey 1987; Clutton-Brock 1989; Chap. 9, this volume), competition for local resources (Clark 1978; Greenwood 1980; Waser 1985), and competition for local mates (Hamilton 1967; Dobson 1982; Moore and Ali 1984). Cooperation among kin may also play an important role in sex-biased dispersal (Perrin and Lehmann 2001; Le Galliard et al. 2006).

Long-term studies regarding a particular bonobo group based on individual identification can provide valuable data for the evaluation of the factors that facilitate and the evolutionary explanations for female dispersal. In this paper, we begin by reexamining the tendencies toward female dispersal in the E1 group at Wamba by reviewing the data from 1976 to 2013. Data regarding intergroup transfer in the E1 group until 2006 have already been published (Furuichi 1989; Kano 1992; Hashimoto et al. 2008), and we add data obtained between 2007 and the end of 2013 in this paper. We then review the patterns of female transfer between unit groups, such as the ages at transfer and the role of intergroup encounters. Although the manner in which immigrant females establish their social position in a new group is an important issue related to the formation of female bonding and dominance relationships between females and males, only three cases of social interactions of immigrant females with resident individuals have been reported (Furuichi 1989; Idani 1990). In the third section, we describe the social interactions of two new immigrant females with resident individuals from their time of immigration to their first birth. We focus on the social associations, dominance relationships, and affiliative interactions of the two new immigrants. Finally, in the last two sections, we summarize the tactics of immigrant females and discuss which of the traditionally proposed factors best explain why female bonobos transfer between unit groups.

Study Subjects and Observation

Bonobos at Wamba

The bonobos at Wamba in the northern sector of the Luo Scientific Reserve in DRC have been studied since 1973 (Kano 1992; Hashimoto et al. 2008; Furuichi et al. 2012). Researchers identified all members of the main study group, “E,” by 1976. Two subgroups (a southern one and a northern one) have been present in the E group since the beginning of the study, and they were known by researchers as two independent groups (“E1” and “E2,” respectively) until 1984. The primary focus of our study was the E1 group, which refers both to the southern subgroup of E group and to E1 group itself. Although artificial provisioning was initially used for detailed behavioral observations, this practice was abolished in 1996 when civil war prevented research in this area. Observations of E1 group resumed in 2003 and have since been conducted under natural conditions. When research resumed, we found that the previously adjacent B and K groups that had ranged in E1’s eastern areas had disappeared, probably because of poaching.

Although we had also studied a western adjacent group, “P,” until 1996, we resumed intensive habituation and daily following of this group in September 2010. We then named one adjacent group “Pe” and another “Pw,” as the latter ranged in the western part of the area ranged by the Pe group. All the individuals in the Pe group were identified by August 2011. As described in detail below, the E1 group had gradually been expanding its home range toward the east at least since 2003, and the E1 group encountered the eastern adjacent group in 2008, probably for the first time. We named this the “Iy” group; members have not been habituated or identified.

Since 2003, the researchers and trained local assistants who had identified all the bonobos in E1 group have usually followed the largest party from one sleeping site (around 0600 h) to the next (around 1700 h). We recorded individual attendance on a daily basis, and the *ad libitum* behaviors of bonobos were directly observed while we followed them. Age groups were defined as follows (Hashimoto 1997): infants (<4 years old), juveniles (4 to <8 years old), adolescents (8 to <15 years old), and adults (15 years or older). When adolescent females gave birth to their first infant, they were considered adults.

Two New Immigrant Females

We analyzed the social interactions of two nulliparous immigrant females, Fuku and Otomi, based on observational data collected by one of the authors (TS) with support from local assistants. In April 2008, while the E1 group ranged to the west and encountered the Pe group (and probably the Pw group as well), a young nulliparous female (probably Fuku) started to range with the E1 group. In June 2008, while the E1 group ranged within the eastern part of their home range, another young

nulliparous female (probably Otomi) that may have been from the Iy group started to range with this group. When the E1 group traveled away from the adjacent groups after this encounter, other unknown individuals that had been observed in the E1 group returned to their groups. However, the two young females mentioned above continued to range with the E1 group. These two females were named Fuku and Otomi on October 14, 2008. At that time, we estimated Fuku to be 10 years old (born in 1998) and Otomi to be 11 years old (born in 1997). After about 2.5 years, on January 6, 2011, and January 11, 2011, we confirmed the first infants born to Fuku and Otomi, respectively.

Behavioral data regarding Fuku and Otomi were collected during four periods between their immigration and their first birth: period 1 (P1) lasted from August 28, 2008, to January 6, 2009; period 2 (P2) from July 4, 2009, to November 23, 2009; period 3 (P3) from June 19, 2010, to August 8, 2010; and period 4 (P4) from October 21, 2010, to February 14, 2011. The observations made during P1 were collected over 574.8 h spread across 76 days, those during P2 covered 447.1 h spread across 65 days, those in P3 were made in 47.4 h spread across 5 days, and those made in P4 were made in 188.3 h spread across 22 days. Observation time was limited in P3 because a researcher (TS) started a survey on other groups at Wamba and in another adjacent population in 2010.

Definitions and Measurements

Daily Social Association and Association Rate

Daily social association (DSA) refers to instances in which group members were observed following the party at least once on a given day. We calculated the DSA values of adult individuals relative to the total number of adult members of the E1 group. The calculation of this DSA ratio included only data collected on days in which we followed the bonobos for almost the entire day or from one sleeping site to the next (whole-day data).

We also calculated the association rates (ARs) of Otomi and Fuku within the observation party. When we directly observed that a target (i.e., Otomi or Fuku) engaged in an association at least once while following a party on a given day, we counted the day as an “association day” for the target. We used only the whole-day data in these calculations. The AR of a target was calculated by dividing the number of her association days by the number of days for which whole-day data were available.

Agonistic Interactions

Agonistic interactions have aggressive components and submissive components; Aggressive components involve *attacking*, *hitting*, *kicking*, *charging*, *chasing*,

charging displays, threats, dragging branches, leaping, running, shaking branches, bending shrubs, and contest hooting. Submissive components include *fleeing, grinning, screaming, peep yelping, other submissive vocalizations, and avoiding* (see de Waal 1988 and Nishida et al. 1999 regarding italicized terms).

We classified agonistic interactions into three types. The first type included interactions in which dominance was clear due to the aggressive and/or submissive behaviors involved. The second type included agonistic interactions in which dominance was unclear. For example, individual *A* rapidly attacked, charged, or enacted a charging display toward another individual, *B*, but *B* did not flee or engage in avoidance, or individual *A* engaged in a charging display (e.g., dragging a branch close to *B*), but *B* did not flee or show submission even though *B* moved a few meters away. The third type involved agonistic interactions that reflected an equal relationship between the participants. For example, individual *A* charged toward or pretended to chase another individual, *B*, and even if *B* initially fled, *B* immediately returned to chase or charge *A*.

It was sometimes difficult to identify the participants in agonistic interactions, especially when the bonobos were in high trees. Therefore, our data were not sufficient to evaluate the frequency of the agonistic interactions involving each individual. The observational data from P3 were not suitable for comparison with those of other periods (P1, P2, and P4) because of reduced observation time during this phase.

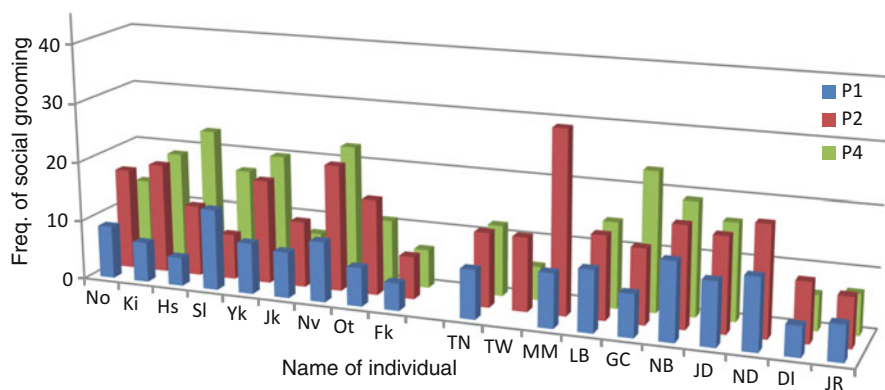
Frequency of Affiliative Interactions

We focused on four types of affiliative interactions: social grooming, social play, genito-genital (GG) rubbing, and copulation. First, we divided our continuous observations into 1-h observation units (OUs). Data from OUs that included less than 40 min of actual observations were excluded from the analyses. When a researcher visually observed an individual, *A*, at least once in one OU, we counted the OU as one for individual *A* (OU-*A*). Table 6.1 presents the number of OUs for each adult and adolescent individual.

Second, in terms of social grooming and social play, if a researcher observed an individual, *A*, engaging in a social interaction *X* (i.e., social grooming or social play) at least once in one OU, we counted the OU as an OU-*A* of social interaction *X* (OU-*A*-*X*). Social interactions between a mother and her own infant (<4 years old) were excluded from the analysis. The frequency with which *A* engaged in interaction *X* (freq-*A*-*X*) was calculated by dividing the number of OU-*A*-*X*s by the number of OU-*A*s. The frequencies are presented in terms of hundreds (Figs. 6.1 and 6.2). With respect to GG rubbing and copulation, a researcher counted the number of *Y* events (*Y* is GG rubbing or copulation). Multi-mounting copulations and multiple GG rubbings were also observed. In such cases, if two or more successive events involving the same participants occurred in a <3-min interval, these events were

Table 6.1 Number of 1-h observation units (OUs) of all adult and adolescent individuals during each study period

		Study period			
		P1 [Oct. 14, 2008, to Jan. 4, 2009]	P2 [July 8, 2009, to Nov. 19, 2009]	P3 [June 28, 2010, to Aug. 6, 2010]	P4 [Oct. 28, 2010, to Feb. 7, 2011]
Total observations (#OU)		334	425	46	177
<i>Female (abbreviation)</i>					
Nao	(No)	90	201	26	119
Kiku	(Ki)	134	223	29	128
Hoshi	(Hs)	125	201	34	116
Sala	(Sl)	198	210	34	136
Yuki	(Yk)	128	201	21	95
Jacky	(Jk)	142	279	32	82
Nova	(Nv)	128	189	10	79
Otomi	(Ot)	108	175	19	83
Fuku	(Fk)	109	237	15	77
<i>Male (abbreviation)</i>					
Ten	(TN)	97	184	28	109
Tawashi	(TW)	0	121	24	106
Mori	(MM)	121	49	–	–
Loboko	(LB)	87	128	26	90
Gauche	(GC)	112	119	12	30
Nobita	(NB)	122	235	33	126
Jeudi	(JD)	94	151	12	43
Nord	(ND)	150	244	–	–
Dai	(DI)	99	150	23	84
Jiro	(JR)	133	240	33	88

**Fig. 6.1** Frequency of social grooming of each adult and adolescent individual during each period (see the text for additional details about the frequency)

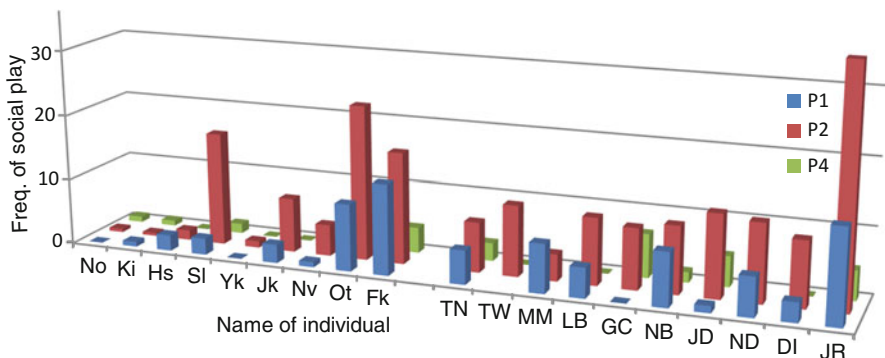


Fig. 6.2 Frequency of social play of each adult and adolescent individual during each period (see the text for additional details about the frequency)

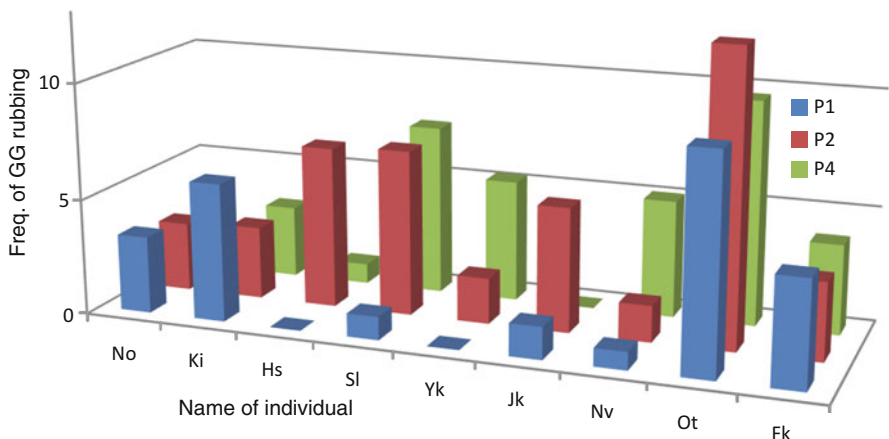


Fig. 6.3 Frequency of GG rubbing of each adult and adolescent female during each period (see the text for additional details about the frequency)

counted as one event. The frequency with which *A* engaged in event *Y* (Freq-*A*-*Y*) was calculated by dividing the number of *Y* acts observed in *A* by the number of OU-As. The frequencies are presented in terms of hundreds (Figs. 6.3 and 6.4). We excluded data from infants and juveniles from the analyses of frequencies.

Sex-Biased Dispersal

Our observational data regarding bonobos at Wamba reflect strong tendencies toward female dispersal during the entire study period. Tables 6.2 and 6.3 present data regarding the life history of the females and males, respectively, in the E1

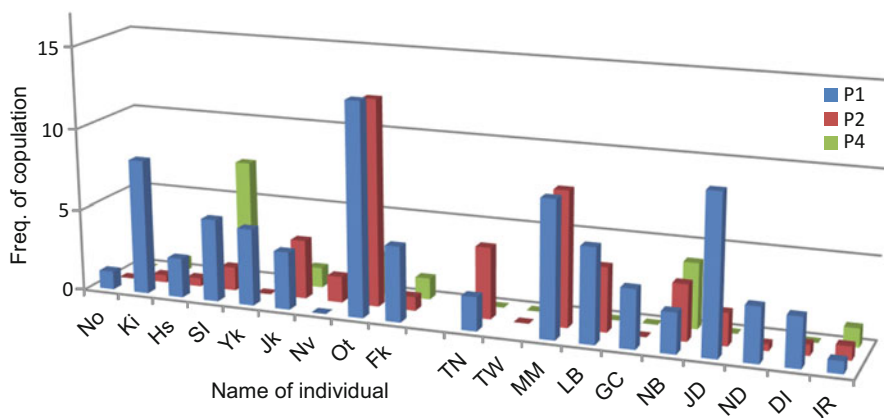


Fig. 6.4 Frequency of copulation of each adult and adolescent female during each period (see the text for additional details about the frequency)

group from 1976 to the end of 2013. The data for the period until the end of 2006 were obtained from Furuichi (1989), Idani (1990), Furuichi et al. (1999), Hashimoto and Furuichi (2001), and Hashimoto et al. (2008) (see also the genetic evidence in Hashimoto et al. 1996). Because observations were not continuous, the data contain gaps regarding births, ages, and the presence of targets. Observations were also interrupted from August 1991 to February 1994 (except during a short visit in August 1992) because of political instability and from June 1996 to August 2003 because of two wars in DRC. Several records maintained by local assistants while the researchers were absent are also included in Tables 6.2 and 6.3.

Identification of the E1 Group and Possible Group Fusion

Eight females and ten males, including immature individuals, belonged to the E1 group when the members of this group were identified before or during 1976. When we resumed our study of the E1 group in 2003, we reidentified members by both direct observation and mitochondrial DNA sequences from fecal samples (Hashimoto et al. 2008; see Tables 6.2 and 6.3). In 2003, the presence of four original members, two females (Nao, Kiku) and two males (Ten, Tawashi), was confirmed. An additional four females and seven males, including immature individuals, were newly identified. The results of DNA analysis suggested that Noire and Nobita were the former Mao and Kikuo, respectively, and that Mori or Jeudi was probably the former Bio (Hashimoto et al. 2008). Further observations of Nobita's relationship with his mother, Kiku, strongly suggested he was Kikuo, but the other identities were not confirmed, as the mothers of Mao and Bio had already disappeared.

Table 6.2 Life histories of females in the E1 group

Name	Birth	Mother	Immigration		Disappearance		Presumed cause
			Time	Age (years)	Time	Age (years)	
<i>1976–1996</i>							
Kame	1945–1950*	?	(Initial member in 1976)		Mar.–Sept. 1990	40–45*	Death by old age
Sen	1945–1950*	?	(Initial member in 1976)		Sept. 1992–Feb. 1994	42–49*	Death by old age
Mitsu	1950–1955*	?	(Initial member in 1976)		Sept. 1992–Feb. 1994	37–44*	Death by old age
Halu	1957*	?	(Initial member in 1976)		1996–2003	39–46*	?
Shiro	1957*	?	(Initial member in 1976)		Aug. 1991–Sept. 1992	34–35*	?
Bihi	1964–1967*	?	Oct.–Nov. 1978	11–14*	1996–2003	29–39*	?
Mayu	1966*	?	(Initial member in 1976)		July 1995–Feb. 1996	29–30*	?
Iku	1971*	?	(Initial member in 1976)		May 1980–Oct. 1981	9–10*	Emigration
Junko	1971*	?	(Initial member in 1976)		May 1980–Oct. 1981	9–10*	Emigration
Nao	1970–1972*	?	Nov. 1983 ^a	11–13*	–	–	–
Miso	1973–1974*	?	Jan. 1984 ^a	9–10*	1996–2003	22–30*	?
Kiku	1974*	?	Dec. 1984 ^a	10*	–	–	–
Shiko	Oct.–Nov. 1978	Shiro	(Native)		Oct. 1987	8	Emigration
Kameko	Mar. 1980	Kame	(Native)		Dec. 1981	1	Death at a young age
Biko	Jan. 1981	Bihi	(Native)		Aug.–Sept. 1989	8	Emigration
Mako	Jan.–Oct. 1981	Mayu	(Native)		Dec. 1988	7	Emigration
Shin	1982*	?	Sept. 1992–Sept. 1994	10–14*	(Alive? Different name after 2003?) ^b		
Balu	1982	Halu	(Native)		Feb.–Sept. 1988	5–6	Emigration or death
Toshi	Mar.–Oct. 1984	Kame	(Native)		Sept. 1992–Feb. 1994	7–9	Emigration
Naomi	Jan. 1985	Nao	(Native)		Feb.–Aug. 1985	0	Death at a young age
Bibi	May 1986	Bihi	(Native)		Sept. 1992–Feb. 1994	6–7	Emigration
Miki	Aug.–Oct. 1986	Miso	(Native)		Sept. 1992–Feb. 1994	5–7	Emigration

(continued)

Table 6.2 (continued)

Name	Birth	Mother	Immigration		Disappearance		Presumed cause
			Time	Age (years)	Time	Age (years)	
Nasa	Sept. 1987	Nao	(Native)		July 1995–Feb. 1996	7–8	Emigration
Miho	Apr. 1990	Miso	(Native)		Sept.–Dec. 1992	2	Death at a young age
Nako	Mar.–Dec. 1993	Nao	(Native)		July–Dec. 1995	1–2	Death at a young age
Midori	Mar.–Dec. 1993	Miso	(Native)		1996–2003	3–10	?
Kino	Mar.–Apr. 1994	Kiku	(Native)		1996–2003	2–9	?
Bina	Jan.–Feb. 1996	Bihi	(Native)		1996–2003	0–7	?
<i>After the resumption of study in 2003</i>							
Hoshi	1981–1985*	?	(Identified in 2003)		–		–
Sala	1991–1992*	?	(Identified in 2003)		–		–
Kirara	1998*	?	(Identified in 2003)		May 2006–Aug. 2007	8–9*	Emigration
Nana	2000*	?	(Identified in 2003)		Sept. 2006–Aug. 2007	6–7*	Emigration
Moseka	1995*	?	(Identified in 2004)		Sept. 2007	12*	Emigration
Yuki	1981–1985*	?	Apr. 2004 ^c	19–23*	–		–
Jacky	1986–1990*	?	Apr. 2004 ^c	14–18*	–		–
Yukiko	2002–2003*	Yuki	Apr. 2004 ^c	1–2*	July 2011	8–9*	Emigration
Nachi	Mar.–Apr. 2005	Nao	(Native)		Feb. 2013	7	Emigration
(No name)	Apr. 2005	Hoshi	(Native)		Apr. 2005	0	Death at a young age
Hina	Feb.–Mar. 2007	Hoshi	(Native)		Dec. 2008	1	Death by flu-like disease ^d
Nova	1994–1995*	?	Aug. 2007	12–13*	–		–

Fuku	1998*	?	Apr. 2008	10*	-	-
Otomi	1997*	?	June 2008	11*	-	-
Nadir	Sept. 2008	Nova	(Native)		-	-
Natsuko	May 2009	Nao	(Native)		-	-
Yume	Oct. 2009	Yuki	(Native)		-	-
Fua	Jan. 2011	Fuku	(Native)		-	-
Otoko	Jan. 2011	Otomi	(Native)		-	-
Zina	2001*	?	Oct. 2011	10*	-	-
Jolie	Jan. 2012	Jacky	(Native)		-	-
Puffy	2003*	(Pao ^e)	Oct. 2013	10*	-	-

*Age estimated

^aSee Furuichi (1989) and Idami (1991)

^bSee Hashimoto et al. (2008) for details

^cPossible group fusion occurred (Hashimoto et al. 2008)

^dSee Sakamaki et al. (2009) for details

^ePao is an adult female in the adjacent Pe group

Table 6.3 Life histories of males in the E1 group

Name	Birth	Mother	Time of identification	Disappearance		Supposed cause
				Time	Age (years)	
<i>1976–1996</i>						
Kake	1945–1950*	?	1976 (initial member)	Jan. 1989	39–44*	Death by old age
Kuro	1950–1955*	?	1976 (initial member)	Aug. 1991–Sept. 1992	36–42*	Death by old age
Hata	1955–1960*	?	1976 (initial member)	June 1991	31–36*	Death by old age
Ika	1960–1962*	?	1976 (initial member)	1996–2003	34–43*	?
Ibo	1962*	Kame	1976 (initial member)	Jan.–Oct. 1987	25*	?
Mon	1967*	Kame	1976 (initial member)	1996–2003	29–36*	?
Goro	1968*	Mitsu	1976 (initial member)	Aug. 1984	16*	Death by poaching
Ten	1970*	Sen	1976 (initial member)	–	–	–
Tawashi	1974*	Kame	1976 (initial member)	–	–	–
Mitsuo	1975*	Mitsu	1976 (initial member)	July 1991–Sept. 1992	16–17*	?
Hahuo	Nov. 1977	Halu	(Native)	Mar.–July 1989	11	?
Senta	Apr. 1980	Sen	(Native)	Sept. 1992–Feb. 1994	12–13	?
Haku	1982	Shiro	(Native)	2002	20	Killed by a soldier ^a
Matsu	Mar.–Oct. 1984	Mitsu	(Native)	Feb.–Sept. 1988	4	Death at a young age
Hayato	Apr. 1986	Halu	(Native)	1996–2003	10–17	?
Mao	Aug.–Oct. 1986	Mayu	(Native, probably identical to Noire in 2003) ^b			–
Shijimi	Feb.–Sept. 1988	Shiro	(Native)	1996–2003	8–15	?
Kikuo	Feb.–Sept. 1988	Kiku	(Native, probably identical to Nobita in 2003) ^b			–
Bio	Feb.–Mar. 1990	Bihi	(Native, probably identical to Mori or Jeudi in 2003) ^b			–
Haze	Mar. 1990	Halu	(Native)	1996–2003	6–13	?
Maro	May 1990	Mayu	(Native)	July 1995–Feb. 1996	5	?

After the resumption of study in 2003

	2002*	Hoshi	2003	Aug. 2004	2*	Death at a young age
Hokuto	1986–1990*	?	2003	–	–	–
Gauche	1986–1990*	?	2003 (probably identical to Mao) ^b	Jan.–May. 2006	16–20*	?
Noire	1991–1996*	(Bihini?)	2003	Aug. 2009	13–18*	Death due to serious injury
Mori	1988*	Kiku	2003 (probably identical to Kikuo) ^b	–	–	–
Nobita	1991–1996*	?	2003	–	–	–
Loboko	1991–1996*	(Bihini?)	2003	–	–	–
Jeudi	1985*	?	Apr. 2004 ^c	Feb. 2010	25*	?
Nord	1975*	?	Sept. 2004 ^c	–	–	–
Dai	2001–2002*	Jacky	Apr. 2004 ^c	–	–	–
Jiro	Feb. 2004	Kiku	(Native)	–	–	–
Kitaro	Nov. 2004	Sala	(Native)	–	–	–
Shiba	Sept. 2006	Jacky	(Native)	–	–	–
Joe	July 2009	Kiku	(Native)	–	–	–
Kyota	Aug. 2009	Hoshi	(Native)	–	–	–
Hachiro	Dec. 2011	Sala	(Native)	–	–	–
Seko	July 2013	Nova	(Native)	–	–	–

*Age estimated

^aSee Furuichi et al. (2012)^bSee Hashimoto et al. (2008)^cPossible group fusion occurred (Hashimoto et al. 2008)

A fusion of unit groups between the E1 group and the formerly adjacent B and/or K groups probably occurred. When we resumed our field study in 2003, we found that most members of the formerly adjacent B and K groups had disappeared, probably because of poaching during periods of political instability and war (Tashiro et al. 2007; Idani et al. 2008; Furuichi et al. 2012). Two adult females and their offspring (Yuki with Yukiko, Jacky with Jiro) and two adult males (Nord, Dai) were initially observed in the E1 group in 2004, when the group ranged in the eastern area, which had been the areas of the formerly adjacent B and K groups. By 2006, they had gradually become stable members of the E1 group. They were thought to be the remnants of the former B and/or K groups (Hashimoto et al. 2008).

Individuals That Disappeared and Newcomers

Three elderly females (Kame, Sen, Mitsu) and three elderly males (Kake, Kuro, Hata) probably died due to old age. Five infant females (Kameko, Naomi, Miho, Nako, Hina) and two infant males (Matsu, Hokuto) disappeared, probably due to death. The carcass of Kameko was confirmed (Kano 1992). Hokuto was an infant that seemed to be skinny and underdeveloped before his disappearance. Hina disappeared during the epidemic of a flu-like disease (Sakamaki et al. 2009).

Among the other females, five adults (Halu, Shiro, Bihi, Mayu, Miso) disappeared for unknown reasons during the researchers' absence. They were stable members with offspring. Because there were no records of the permanent transfer of parous females (see the next section), we assumed that they had died. Three immature females (Midori, Kino, Bina) also disappeared for unknown reasons during the researchers' absence between 1996 and 2003. They may have reached the age of potential emigration by 2003. An additional 15 native females (Iku, Junko, Shiko, Biko, Mako, Balu, Toshi, Bibi, Miki, Nasa, Kirara, Nana, Moseka, Yukiko, Nachi) disappeared from the E1 group before having their first child. We presumed that they had emigrated from the natal group. Nine cases of immigration by females were recorded (Bihi, Nao, Miso, Kiku, Shin, Nova, Fuku, Otomi, Zina). Another young female (Puffy) immigrated in October 2013 and was still present at the end of 2013. All were young nulliparous females when they immigrated to the E1 group. Several strange females with clinging infants were observed in the E1 group when the group encountered or traveled near the adjacent unit groups, but they stayed in the E1 group for a short period of time (see the next section and Table 6.4).

Of the other males, Goro died in August 1984 as a result of poaching, and Haku was killed by soldiers in 2002. Mori disappeared in August 2009, immediately after sustaining a serious injury when he accidentally fell from a tree while performing a charging display. His death must have been a consequence of this serious injury (Behncke and Sakamaki, unpublished data). Six adult males (Ika, Ibo, Mon, Mitsuo, Noire, Nord) and six adolescent males (Haluo, Senta, Hayato, Shijimi, Haze, Maro) disappeared for unknown reasons. Several disappeared during the researchers' absence. Nord seemed to have no health problems before disappearing in February

Table 6.4 Females that temporarily visited the E1 group

Name	Immigration			Period of stay in E1	Accompanying infant
	Birth	Time	Estimated age (years)		
Atsu ^a	1974–1975*	Oct. 1983	8–9	ca. 1 week	None
Mini ^a	1975–1976*	Oct. 1983	7–8	ca. 1 week	None
Kisu ^a	1976–1977*	Aug. 1985	8–9	ca. 1 month	None
Suga ^a	1958–1963*	Sept. 1985	22–27	ca. 2–3 weeks	Yes
Yuki ^{a,b}	1971–1972*	Dec. 1985	13–14	ca. 3 weeks	None
Elu ^a	1960–1965*	Dec. 1985	20–25	ca. 1 week	Yes
Yasa ^a	1956–1961*	Jan. 1986	25–30	ca. 1 week	Yes
Viki ^a	1979–1980*	Jan. 1988	8–9	ca. 1 week	None
Fuku ^{a,b}	1979–1980*	Feb. 1988	8–9	ca. 1 week	None
(No name) ^c		Feb. 1985	(Adolescent)	1 day	None
Shiwa ^c	1979–1980*	Nov. 1988	8–9	ca. 1–2 weeks	None
Pino	2000–2001*	Aug. 2007	6–7	ca. 1 week	None
Zolo	2000–2001*	Aug. 2007	6–7	ca. 3 months	None
Kasa	1985–1990*	Sept. 2008	18–23	ca. 1–2 weeks	Yes
Ana	2001*	Feb. 2011	10	ca. 5–6 months	None
Ana ^d		Aug. 2013		ca. 2–3 months	None

*Age estimated

^aSee Furuichi (1989)^bNote that these two individuals (Yuki, Fuku) differed from the individuals with the same name in Table 6.2^cSee Idani (1991)^dThis was Ana's second visit

2010. These males were not found in other unit groups. With the exception of the possible group fusion mentioned above, there are no records of the immigration of strange males into the E1 group.

Other Study Sites

Among the other study sites with wild bonobos, descriptions of intergroup transfer were found in the previous reports about Lomako. Two nulliparous females immigrated to the “Hedon” group and gave birth by 1991, and one nulliparous female that had been very peripheral in 1985 had become a central parous female in the “Ranger” group by 1991 (White 1996). Between 1993 and 1998, one adult female immigrated to and four adolescent or adult females without infants temporarily visited the “Eyengo” (same as the Ranger) group (Hohmann 2001). Two strange adult males entered the Eyengo group in 1997, and at least one of them remained in the group for at least 11 months, until the end of the study period (Hohmann 2001). During the study period, the number of adult males decreased, whereas the group size and the number of adult females remained relatively stable. In summary, bonobos at Lomako tended toward a pattern of female dispersal (see also genetic evidence: Gerloff et al. 2011), and our data also suggested that male transfer can occur under certain social or ecological conditions (Hohmann 2001).

Patterns of Female Transfer

In this section, we describe several patterns of female intergroup transfer in terms of ages at emigration and immigration, temporary visits, intergroup encounters as opportunities for transfer, second transfers by parous females, and time from immigration to first birth.

Ages at Intergroup Transfer

We assumed that 15 females emigrated from the E1 group (Table 6.2) because they were in a good health during the observations prior to their disappearance, although the immigration of these females to other groups was not confirmed. These individuals ranged from 5 to 12 years at emigration. The oldest émigré was Moseka, who was identified in 2004 after the long interruption in our study, and her age may have been overestimated. If we exclude Moseka, the oldest age at emigration was 9–10 years (Iku, Junko; both ages were estimated). The youngest émigrés, who were 5 years of age, were two females (Balu, Miki). Thus, we estimated that most emigration occurred between 6 and 9 years of age and that this practice was most

common at 5–10 years of age. Although these results are consistent with previous reports (Furuichi 1989; Hashimoto and Furuichi 2001; Hashimoto et al. 2008), these ages are younger than those of emigrating chimpanzees (Mahale, range = 9.7–14.0 years, median = 11, Nishida et al. 2003; Kibale (Kanyawara), 10.4–15.7 years; Gombe, 12–13 years, Emery Thompson 2013).

Older juvenile and adolescent females sometimes remain on the periphery of a ranging party (Hashimoto et al. 2008). One young female, Puffy, sometimes remained on the periphery of the gathering while in her native Pe group in 2012, and she immigrated to the E1 group in October 2013. In contrast, Yukiko and Nachi, who were assumed to emigrate from the E1 group in 2011 and 2013, respectively, did not exhibit a clear tendency to stay on the periphery of a gathering before their emigration. Prior to their departure, the E1 group ranged away from adjacent groups and rarely encountered such groups (e.g., no visual encounters for the nearly 2 years beginning in September 2008). These conditions may have affected their spatial positions in the ranging parties.

Nine females immigrated to the E1 group from other unit groups (Table 6.2). Their estimated age at immigration was between 9 and 14 years. It is sometimes difficult to estimate the age of young females because of individual variations in body size and in the shape of the genital area. However, females aged 6–9 years (ages at emigration) are childlike and small, and their genital area is also obviously small even though it is swollen (Fig. 6.5). We found a gap of a few years between the age at emigration (6–9 years) and that at immigration (9–14 years).

Temporary Visits

In view of the gap between the age at emigration and that at immigration, young females appear to visit several unit groups after leaving their natal group before they finally settle in a new group. Kano (1992) reported that at least 30 young females of other unit groups had contact with the E group from 1976 to 1985, and 25 of these individuals disappeared after intermittent stays of various lengths of time (no data were presented on the lengths of time). The other five females gave birth to their first infants in the E group and became fairly stable group members. In 2013, we observed that one nulliparous adolescent female (Nara) sometimes ranged with the Pe and with the adjacent Pw groups.

Table 6.4 presents data regarding females that temporarily visited the E1 group, usually for about 1 week. The data for the period until about 1988 were drawn from Furuichi (1989) and Idani (1991). These short temporary visits usually occurred when the E1 group encountered or ranged near the adjacent unit groups. The number of females listed in Table 6.4 is limited because not all the temporary visitors were identified. We also confirmed the presence of other unknown individuals in the E1 group when adjacent unit groups encountered and ranged near the E1 group (Kano 1982, 1992; Idani 1990; this study).



Fig. 6.5 *Upper left*: a temporary visitor, Zolo, on September 7, 2007. *Upper right*: Fuku on November 25, 2008. *Lower left*: Fuku and her first infant on August 29, 2011. *Lower right*: Fuku on August 29, 2011

Although most of the females listed in Table 6.4 were nulliparous and young, four had clinging infants (Suga, Elu, Yasa, Kasa). They were observed in the E1 group for 1–3 weeks. When the E1 group ranged away from adjacent groups, they returned to the adjacent groups. With the exception of Yuki and Jacky (during the possible group fusion), there were no records of parous females immigrating to and settling with the E1 group.

The cases of Zolo and Ana differed from those of other temporary visitors in terms of the length of their stay, as they remained in the E1 group for a relatively long duration, a few months or more. Zolo joined the E1 group when it encountered the Pe group in August 2007, and she continued to stay in the group when it ranged away from the Pe group. She disappeared from the E1 group in December 2007. Ana stayed in the E1 group for 5.5 months, beginning in February 2011. She was probably from the Iy group, as we first confirmed her presence in the eastern area of the range of the E1 group. She disappeared from the E1 group but returned to the group after about 1 year. After an approximately 2-month stay in the E1 group, she disappeared again. [Her return to E1 was again confirmed in 2014, although this study presents only data gathered until the end of 2013.]

Opportunities for Transfer

Intergroup transfer usually occurs when two unit groups encounter and range closely to each other. Therefore, the opportunity for transfer increases when bonobos range in an area that overlaps with that of adjacent groups. In this sense, overlap supports the maintenance of the social structure (Kano 1982, 1992; Idani 1990).

Because the E1 group has been in a special situation since the resumption of our study in 2003, our observations provide important information about the relationship between intergroup encounters and female transfer. After the extinction of the adjacent B and K groups, the E1 group markedly expanded its home range toward the east and changed the area it frequently ranged (Tashiro et al. 2007; Idani et al. 2008; Sakamaki et al. unpublished data). As a result, opportunities for intergroup encounters have decreased. For example, the E1 group had not encountered adjacent groups during the approximately 22 months from September 2008 to July 2010. During this period, we did not observe any newcomers enter E1 group. Although the bonobos of E1 group exchanged vocalizations (but not visual contact) with the Iy group on August 31 and September 17–18 of 2009 in an area farther to the east, we did not confirm the presence of any unfamiliar bonobos in the E1 group. This very rare case at Wamba shows that young females do not travel alone to an adjacent group in distant area.

Second Transfer

There has been no evidence of a second transfer between unit groups by parous females at Wamba. After giving birth to their first infants in the E1 group (Bihi, Nao, Miso, Kiku, Nova, Fuku, Otomi), immigrant females became fairly stable members of that group. The presence and first birth of another immigrant nulliparous female (Shin) were not confirmed because of the researchers' long absence during the war. Before 1991, when political disorder began, no parous female, except for Kame,

who probably died of old age, was noted. Sen and Mitsu, who disappeared during the researchers' absence from 1992 to 1994, may have died of old age. Parous Bihi and Miso disappeared during the researchers' long absence between 1996 and 2003.

From Immigration to First Birth

The median time between immigration and first birth was 30 months (range = 12–45 months). The first births of eight of nine immigrant females were confirmed (Table 6.5). At least Miso and Kiku seemed to sometimes visit other unit groups between immigrating and their first birth (Idani 1990). The data regarding these 30 months are similar to those of chimpanzees (approx. 2–3 years; in review, Emery Thompson 2013).

Two New Cases of Immigrant Females

This section describes the social interactions of two new immigrant females, Otomi and Fuku. Their behaviors were observed from the time of their immigration to their first birth. The first part focuses on their DSA rate, and the next describes dominance relationships between the new immigrant females and resident individuals. In the third part, we present the data regarding their affiliative interactions, social grooming, social play, GG rubbing, and copulation.

Associational Patterns of New Immigrants

At first, Otomi and Fuku almost always associated with most of the resident individuals in the main party of the E1 group. The two bars on the left-hand side of each period represented in Fig. 6.6 show the DSA rates of adult individuals (white and light-gray bars indicate adult males and adult females, respectively). More than 80 % of the adults in the E1 group were observed on most days, with the exception of P1b. This means that almost all members of the E1 group usually ranged together; even if they were scattered to some degree, they were probably within earshot (Fig. 6.7). During P1b, many individuals showed symptoms of a flu-like disease, and they divided into small parties for approximately 3 weeks in December 2008 (Sakamaki et al. 2009). The two bars on the right-hand side in each period depicted in Fig. 6.6 show the AR in the observation party (dark-gray and black bars indicate Otomi and Fuku, respectively). When the DSA rate was high, Otomi and Fuku were observed primarily in the observation party. When the AR was low (in P1b), the DSA rate was also low. During this time, Otomi and Fuku probably ranged alone or with other members that had separated from the observation party.

Table 6.5 Period between immigration and first birth

Name	Time of immigration	Time of first birth	Name of first offspring	Period (months) until the first birth
Bihi	Oct.–Nov. 1978	Jan. 1981	Biko	26–27
Nao	Nov. 1983	Jan. 1985	Naomi	14
Miso	Jan. 1984	Aug.–Oct. 1986	Miki	31–33
Kiku	Dec. 1984	Feb.–Sept. 1988	Kikuo	38–45
Nova	Aug. 2007	Sept. 2008	Nadir	12–13
Fuku	Apr. 2008	Jan. 2011	Fua	33
Otomi	June 2008	Jan. 2011	Otoko	31

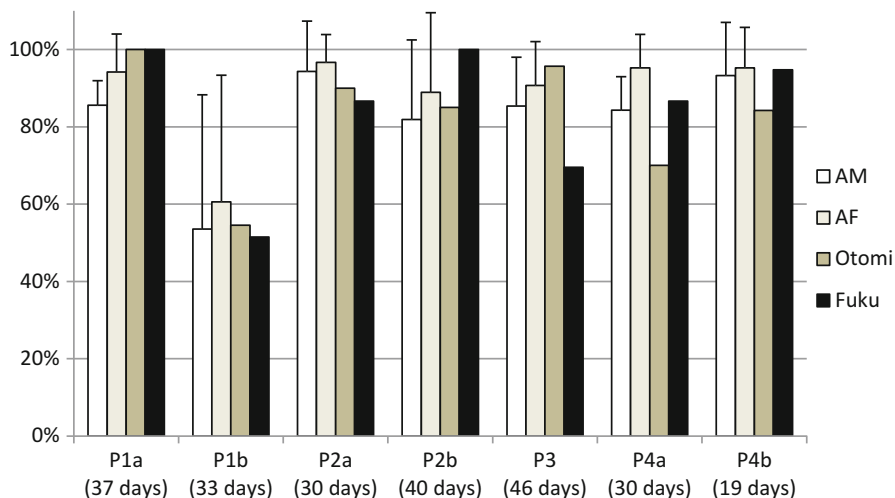
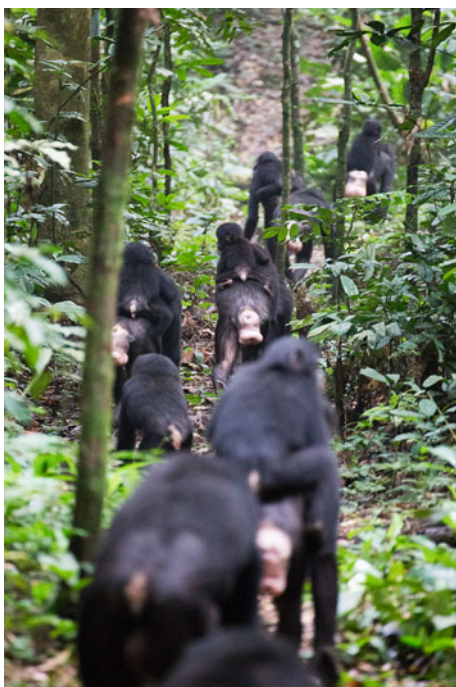


Fig. 6.6 Mean and *SD* of the daily social association (DSA) value relative to the total adult members of the E1 group (the two bars on the left side, *white* and *light-gray* bars, indicate adult males (AMs) and adult females (AFs), respectively) and association rate (AR) of Otomi and Fuku in the observation party (the two bars on the right, *dark-gray* and *black*, indicate Otomi and Fuku, respectively). The numbers in *parentheses* indicate the number of the days in each period. We analyzed only the days on which the bonobos were followed for almost the entire day

Fig. 6.7 Females walking with their offspring



Otomi and Fuku rarely visited other unit groups during the approximately 2.5 years from their immigration to their first birth. However, they may have visited other unit groups before we identified them in 2008. There were four periods in which Otomi or Fuku was absent from the large observation party for several successive days. First, Fuku was absent when most E1 members were observed on August 5–10, 2009. As noted above, an adult male, Mori, was seriously injured on August 4, 2009, and disappeared. All other members were observed during every day. Fuku may have ranged alone or with the injured Mori. Second, Fuku was absent while almost all E1 members were observed from January 27 to February 5, 2010. Immediately before and after this period, the E1 group separated into relatively small parties. Thus, Fuku may have ranged with another small party. Third, Fuku was absent when almost all E1 members ranged together from July 23 to August 4, 2010. During this time, the E1 group repeatedly encountered the Iy group. Another adult female, Nova, was also absent during this period, and we suspected that Fuku and Nova ranged with individuals from the Iy group. Fourth, Otomi was absent when we followed a relatively large party from November 25 to December 4, 2010. During this period, a few other individuals, including Fuku, were only intermittently present in the observation party. Otomi may have ranged with others in separate small parties.

Dominance Relationships Between Immigrants and Residents

In bonobo societies, the dominance relationship between males and females is equivocal or characterized by equality, and females seem to be dominant over males in the context of feeding (White and Wood 2007; Furuichi 2011). Because new immigrant females are usually observed on the periphery of a gathering and do not have high social status at the beginning, the process by which immigrant females establish their social position in a new group is of great interest. We examine this process based on our observations of Otomi and Fuku.

Figure 6.8a–c shows the direction of three types of agonistic interactions during P1, P2, and P4, respectively. As mentioned above, our observational data were not sufficient for estimating the frequency of agonistic interactions because only some of the participants in the interactions were identified. However, agonistic interactions including Otomi and Fuku were observed primarily during P2. Some, but not all, adult females exerted dominance over Otomi and Fuku, but not vice versa. In contrast, males exerted dominance over Otomi and Fuku in some interactions, but Otomi and Fuku also exerted dominance over males in other interactions. In other words, Otomi and Fuku were subordinate to resident females, whereas they were equal to or had equivocal relationships with resident males.

We observed several cases in which Otomi and Fuku appeared to challenge adult males. Interestingly, they behaved playfully in such instances. In the scene described below, we observed both an aggressive attitude and a playful mood.

Aggressor	Receiver																										
	NB	MM	ND	TN	GC	JD	DI	LB	TW	JR	Kitaro	Shiba	Joe	No	Ki	Hs	SI	Yk	Jk	Nv	Oi	Fk	Yukiko	Nachi	Hina	Nadir	
AM NB	X	ΔΔ	Δ	EO	OAA ΔOO	OOΔ OO	O			O																	
AM MM		X	O	ΔIΔ	ΔIO	Oi	O																				
AM ND			X		O	Oi																					
AM TN	E			X	O	O	Δ																				
AM GC					X	O	O																				
AM JD						X	O	O																			
AM DI							X	O																			
AM LB							O	X																			
AM TW								X																			
JM JR									X																		
JM Kitaro										X																	
I-JM Shiba											X																
IM Joe												X															
AF No		O											X														
AF Ki		O					O	OOO							X												
AF Hs								OIO								X											
AF SI								OIO									X										
AF Yk								OIOO										X									
AF JK								Oi											X								
AF NV																				X							
SF Oi																					X						
SF Fk																						X					
SF Yukiko																							X				
IF Nachi																								X			
IF Hina																									X		
IF Nadir																										X	

Fig. 6.8 (continued)

b	P2	Receiver																																				
		Aggressor	NB	TN	MM	GC	JD	ND	LB	DI	TW	JR	Kitaro	Shiba	Joe	Kyota	Hachiro	No	Ki	Hs	SI	Yk	Jk	Nv	Ot	Fk	Yukiko	Nachi	Hina	Nadir	Yume							
AM	NB	X	Δ	O	OOO																																	
AM	TN		X				OO			OO																O												
AM	MM			X	OOO																																	
AM	GC				X			ΔO																														
AM	JD				X	EOO			OΔΔ																													
AM	ND					EO	X		OO																													
AM	LB							X	O	OΔ																												
AM	DI								X																													
AM	TW									X																												
AM	TW										X																											
SM	JR										X																											
JM	Kitaro											X																										
JM	Shiba												X																									
JM	Shiba													X																								
IM	Joe														X																							
IM	Kyota															X																						
IM	Hachiro																X																					
AF	No																	X																				
AF	Ki																		X																			
AF	Hs																			X																		
AF	SI																				X																	
AF	Yk																					X																
AF	Jk																						X															
AF	Nv																							X														
SF	Ot																								X													
SF	Fk																									X												
SF	Yukiko																										X											
JF	Nachi																										X											
JF	Hina																										X											
IF	Nadir																											X										
IF	Yume																												X									

Fig. 6.8 (continued)

C P4

Aggressor	Receiver																											
	NB	TN	DI	GC	TW	LB	JD	JR	Kilaro	Shiba	Joe	Kyota	Hachiro	No	Ki	Hs	SI	Yk	Jk	Nv	Ot	Fk	Yukiko	Nachi	Hina	Nadir	Yume	
AM	NB	X	ΔO	OI			OOI										Δ											
AM	TN	X	O	OIO	Δ		O	O														O						
AM	DI		X	O			O																					
AM	GC			X																								
AM	TW				X	O																						
AM	LB				X	O																						
AM	JD					X	O																					
SM	JR						X																					
JM	Kilaro							X																				
JM	Shiba								X																			
IM	Joe									X																		
IM	Kyota										X																	
IM	Hachiro											X																
AF	No													X														
AF	Ki														X													
AF	Hs															X												
AF	SI																X											
AF	Yk																	X										
AF	Jk																		X									
AF	Nv																			X	OI	OI						
AF	Ot																				X	O						
SF	Fk																					X						
SF	Ot																						X					
SF	Fk																							X				
JF	Yukiko																							X				
JF	Nachi																								X			
IF	Hina																									X		
IF	Nadir																										X	
IF	Yume																											X

Fig. 6.8 Dominance relationships based on the direction of behaviors in agonistic interactions (see the text for further details). Panels (a–c) are during P1, P2, and P4, respectively. “O” indicates agonistic interactions in which dominance was clear due to aggressive and/or submissive behaviors. If two or more aggressors or two or more receivers participated in the agonistic interactions, “O” was coded (e.g., when two aggressors attacked one receiver, two cells were marked). “Δ” indicates the agonistic interactions in which dominance was unclear. “E” indicates the agonistic interactions that reflected equality between/among participants (i.e., in such cases, both cells are marked for each participant). “AM” and “AF” indicate adult male and female, respectively (15 years or older). “SM” and “SF” indicate adolescent male and female, respectively (8 to <15 years old). “JM” and “JF” indicate juvenile male and female, respectively (4 to <8 years old). “IM” and “IF” indicate infant male and female, respectively (<4 years old)

Scene 1 (August 19, 2009)

Beginning at 0703 h, a large party (seven adult males, four adult females, Otomi, Fuku, and immature individuals) remained in a clearing created by felled trees. Several dyads were engaged in grooming. At 0736 h, Otomi charged toward one adult male (Dai), and he fled. At 0737 h, Dai emitted a contest-hooting utterance and charged toward Otomi, and she fled. Dai continued contest hooting and sometimes engaged in charging displays. At 0740 h, Dai issued a contest-hooting utterance and engaged in a charging display, and Otomi charged toward Dai, who then fled to a tree. At 0742 h, while Dai continued contest hooting and engaging in charging displays, a juvenile female (Yukiko) approached him as if inviting him to play. At 0744 h, Yukiko, another juvenile female (Nachi), and a juvenile male (Shiba) approached Dai while playing with one another, although Dai emitted contest-hooting utterances and repeatedly engaged in charging displays. At 0746 h, another adult male (Nord) approached to groom Dai, but Dai moved away from him and sat 5 m from Nord. At 0748 h, Otomi approached Nachi, who was playing with Yukiko and Shiba. At 0749 h, Dai again issued contest-hooting utterances and engaged in a charging display, and Otomi chased Dai. Several adult individuals continued grooming, and immature individuals continued playing.

In this scene, many bonobos were resting in a clearing. Several adults engaged in social grooming, and immature individuals played with one another. During this period, Dai exhibited aggressive intentions, as evidenced by behavior such as charging, charging displays, and contest hooting. In response to such aggression, Otomi sometimes fled and sometimes charged toward Dai. Otomi's behaviors in this context seemed to be playful rather than serious. Other immature individuals also behaved playfully and appeared to enjoy chasing and wrestling with one another. During this time, Dai was the only individual that attempted to show his dominance over others. Although Genty et al. (2014) argued that bonobos at the "Lola ya Bonobo" sanctuary used contest hooting in two opposite contexts, agonistic and friendly, Dai's behaviors in this scene were clearly aggressive and contrasted with the playful behaviors of other individuals. Thus, immature individuals, including Otomi, reacted playfully to the aggression exhibited by Dai in this scene.

Social play also sometimes escalates into aggression. Such aggressiveness in playful interactions was also observed. For example, during P2, we observed increasingly aggressive behaviors by Sala (adult female) against Otomi and Fuku while they actively engaged in chasing play. In such scenes, we sometimes observed dominance relationships between participants. Again, it was sometimes difficult to distinguish aggressive from playful behaviors in such situations.

In this way, actual dominance relationships in bonobos appeared not only in clear-cut agonistic interactions but also in prolonged playful interactions. These playful interactions indicate that their dominance relationships are ambiguous rather than rigid. First, wrestling and chasing, in which participants change roles (e.g., chasing and fleeing), are frequent forms of play. Second, when a larger, older, or dominant individual plays with a smaller, younger, or subordinate individual, the former does not use his/her full strength but matches his/her strength to that of the

Social grooming																				
Adult females										Adult males										
Ot	No	Ki	Hs	Sl	Yk	Jk	Nv	Ot	Fk	TN	TW	MM	LB	GC	NB	JD	ND	DI	JR	
P1	1	1	0	0	1	1	0	X	0	0	--	0	0	0	0	0	0	0	1	
P2	0	0	0	1	1	3	2	X	3	0	0	0	4	0	0	2	1	1	1	
P4	1	0	0	1	2	0	0	X	1	1	0	--	0	0	2	1	--	1	0	
Fk										Fk										
P1	0	0	1	0	1	0	0	0	X	1	--	0	0	0	0	0	0	0	0	
P2	2	0	1	0	0	0	1	3	X	0	0	0	0	0	1	1	2	0	0	
P4	0	0	0	0	0	0	0	1	X	0	0	--	2	0	1	1	--	0	0	
GG rubbing										Copulation										
Adult females										Adult males										
Ot	No	Ki	Hs	Sl	Yk	Jk	Nv	Ot	Fk	Ot	TN	TW	MM	LB	GC	NB	JD	ND	DI	JR
P1	2	3	0	2	0	0	0	X	0	1	--	4	1	2	0	1	0	2	0	
P2	2	0	4	4	0	2	1	X	4	2	0	0	4	0	4	2	1	1	1	
P4	0	0	1	4	1	0	0	X	2	0	0	--	0	0	0	0	--	0	0	
Fk										Fk										
P1	0	4	0	0	0	0	0	0	X	1	--	1	0	0	0	1	1	0	0	
P2	0	0	0	1	1	1	0	3	X	0	0	2	0	0	0	0	0	0	0	
P4	0	0	0	1	0	0	0	2	X	0	0	--	0	0	0	0	--	0	0	

Fig. 6.9 Social grooming and GG rubbing and copulation involving Otomi and Fuku during each period. The number of events observed is presented in each cell

latter. Such a tactic while playing is called “self-handicapping” (Fagen 1981; Hayaki 1985; Enomoto 1990). Therefore, social play consists of a kind of reciprocal and symmetrical interaction, and this feature leads to relatively benign and ambiguous dominance relationships among participants.

Affiliative Interactions

The frequency with which every adult and adolescent engaged in affiliative interactions (i.e., social grooming, social play, GG rubbing, and copulation) in each period (except for P3, because of the brief period of observation) is presented in Figs. 6.1, 6.2, 6.3, and 6.4. Otomi’s and Fuku’s partners in social grooming, GG rubbing, and copulation are presented in Fig. 6.9.

All adult and adolescent individuals engaged in social grooming to some extent (Fig. 6.1). Otomi and Fuku engaged in social grooming, which is among the most common social behaviors among bonobos and contributes to the maintenance of social bonds (Kano 1992; Sakamaki 2013), during each period. However, their partners in social grooming seemed to change from P1 to P2 (Fig. 6.9). Otomi and Fuku groomed primarily with adult females in P1 but rarely did so with adult males. Their engagement in social grooming with adult males started in earnest during P2.

Otomi and Fuku engaged in social play more frequently than other adult individuals did (Fig. 6.2), whereas an adolescent male (Jiro) also did so frequently. Figure 6.2 shows that more adult males than adult females engaged in social play on a frequent basis, although Sala and Jacky frequently engaged in social play during P2. Because we did not maintain records of all the immature individuals that engaged in social play, Fig. 6.2 presents the data for only adolescent and adult individuals. However, juveniles frequently engaged in social play (Fagen



Fig. 6.10 Adult and adolescent females grooming

1981; de Waal 1988; Kano 1992), and we sometimes observed many individuals simultaneously involved in social play.

Otomi engaged in GG rubbing more frequently than Fuku did during each period (Fig. 6.3), although Fuku also engaged in this activity. Additionally, the frequency with which adult females engaged in this activity differed across periods. For example, Hoshi, Sala, and Jacky engaged in GG rubbing more frequently during P2 than during P1. Although more studies are needed before conclusions can be drawn, this may be related to the ages of their infants and their reproductive status. Otomi also engaged in copulation more frequently than did Fuku (Fig. 6.4), and Otomi had more partners in GG rubbing and copulation than did Fuku (Fig. 6.9). No copulation with adult males was observed during P4, probably because of their pregnancy. Copulation with juvenile males was observed during P4.

In summary, during the initial stage of immigration, Otomi and Fuku engaged in social grooming with resident females but rarely did so with adult males. At the beginning, they appeared to regard social bonding with resident females as more important than bonding with males (Fig. 6.10). Copulation is a main medium through which immigrant females can interact with adult males immediately following their arrival. Otomi was more active in regard to copulation and GG rubbing than was Fuku. Indeed, there may be consistent individual differences in sexual and sociosexual activities. Additional research is needed regarding the effects of such differences on future social positions. Otomi and Fuku engaged in social play more frequently than did resident adults, indicating that females at the age of immigration remain childlike in some respects. Given its commonality, social play serves an important role in establishing social bonds between immigrant females and resident individuals.

Tactics of Immigrant Females

What is the cost of immigration for immigrant females? In chimpanzee societies, aggression perpetrated by resident females is costly to immigrant females; however, although severe aggression sometimes occurs, males are effective in protecting immigrant females (Nishida 1989; Kahlenberg et al. 2008a, b; Pusey et al. 2008). The establishment of close relationships with particular resident females is an effective strategy with which immigrant chimpanzee and bonobo females improve their social position in a new group (Furuichi 1989; Idani 1991; Nishida 2012). In what follows, we first summarize the dominance relationships and associations of Otomi and Fuku with particular females. Next, we underscore the importance of social play for immigrant females. Finally, we discuss the absence of a second transfer among parous females.

Dominance Relationships with Residents

Aggression by resident females toward Otomi and Fuku was observed, especially during P2, suggesting conflict between resident and immigrant females. As a result of these agonistic interactions, Otomi and Fuku assumed a low position among the adult females of the new group. Interestingly, no agonistic interactions were observed among resident adult females during the study periods, although such interactions were sometimes observed between adult females and males. In bonobo society, dominance relationships among adult females are rarely manifested in agonistic interactions, whereas the subordination of immigrant females to resident females is manifested in agonistic interactions.

Instances of copulation between immigrant females and adult males were observed from the arrival of the former. Copulation is an important way to establish tolerance and bonding between immigrant females and resident males (Idani 1990). On the other hand, no male protection of immigrant females from aggression perpetrated by resident females was observed. This may be related to the dominance relationship between males and females, as adult males cannot easily overcome adult females (White and Wood 2007; Furuichi 2011).

Our observations showed that dominance relationships between immigrant females and resident males were sometimes unclear or equivocal (Fig. 6.8). In *Scene 1*, an immigrant female, Otomi, exhibited a competitive attitude toward an adult male, Dai, while Dai persistently tried to show his dominance over Otomi. However, Otomi responded to this aggression with a playful attitude. Neither Dai nor Otomi lost. The relative absence of males outranking females is a conspicuous feature of a bonobo society that contributes to the establishment of the social position of immigrant females in a new group.

Association with Particular Females

Female bonding is a key feature of bonobo society. Previous studies have shown that immigrant females frequently approached, followed, and engaged in affiliative interactions with a specific senior female (SSF) (Furuichi 1989; Idani 1991). We did not find clear an SSF for Otomi and Fuku, but our data may be lacking in this regard, as we did not record behavioral data in the same way as we had in previous studies (i.e., focal animal sampling). However, we did not observe a close association between Otomi or Fuku and a particular female that lasted for at least a few days. Some immigrant females are closely associated with an SSF for a relatively long period of time (Furuichi 1989; Idani 1991), suggesting that individual differences may affect the extent to which immigrant females rely on particular resident females.

Otomi and Fuku appeared to engage in social interactions with most resident females. Social association with resident individuals may be essential for immigrant females to establish affiliative bonds in a new group. The relatively high DSA rates and ARs indicate that Otomi and Fuku ranged with most members of the E1 group almost every day. These activities offered opportunities for them to engage in various interactions with resident individuals, and they frequently played with immature individuals. Most playmates were offspring of resident females. Moreover, GG rubbing between immigrant and resident females was observed from the beginning of the arrival of the immigrants. Frequent GG rubbing occurs at feeding sites, as bonobos become excited in response to large quantities of ripe fruits, leading females to engage in GG rubbing with each other. This reduces their tension, and they then eat together. GG rubbing enables female bonobos to tolerate and peacefully coexist with one another in potentially conflictual situations to a greater extent than males are able to do (Hohmann and Fruth 2000; Ryu et al. 2014).

Social Play

We now focus on the role of social play as a tactic for immigrant females. First, the female bonobos that transferred between unit groups were younger than the chimpanzees that did so. Second, Otomi and Fuku engaged in social play more frequently than did adult individuals. Generally, juveniles engage in social play much more frequently, and younger immigrant females are more likely to engage in social play (Fagen 1981; de Waal 1988; Kano 1992). Because immigrant females are still childlike at the time of their immigration (Fig. 6.5), they frequently play with immature individuals in a new group. At times, many individuals are simultaneously involved in social play. Thus, social play accounts for a relatively large part of the social interactions between immigrant females and resident individuals in a new group.

Dominance relationships are sometimes observed in social play, and this can escalate into aggression. We also observed an immigrant female exhibiting a competitive but playful attitude toward an aggressive adult male. Dominance relationships in such playful interactions may also be related to the mild and simple forms of aggression among bonobos (Kuroda 1980). Adult bonobos appear to engage in social play more than do adult chimpanzees (Enomoto 1990; Palagi 2006). It is also important to note that social play consists of reciprocal and symmetrical interactions; that is, participants sometimes change roles (e.g., chasing and fleeing) and self-handicap during social play. Reciprocal and symmetrical interactions contribute to the establishment of symmetrical or equal relationships among participants. It is also important to note that GG rubbing is a kind of symmetrical interaction. Socially symmetrical relationships are the basis for the egalitarianism of bonobo society (Enomoto 1990; Palagi 2006). During the process of establishing their social positions in a new group, childlike immigrant females appear to embody the typical features of bonobo society.

Absence of Second Transfer

With the exception of a case of group fusion and despite the risk of mother–son incest and the absence of infanticide, there is no evidence of second transfer by parous females. Intergroup encounters present opportunities to transfer between unit groups. Adult females with clinging infants sometimes enter another unit group and may stay for a week, but they return to their own group when the two unit groups range far from each other. The absence of a second transfer by parous females may be related to the practice of intimate female bonding. Once a female acquires her social position in a new group, she may want to maintain a close association with other females in the group. Furthermore, mother–son relationships are related to the absence of parous female transfer in that mothers can increase the number of their grandsons if they can provide effective support for their sons (Furuichi 1997; Surbeck et al. 2011).

Why Do Female Bonobos Transfer Between Groups?

Our observations of bonobos at Wamba from 1976 to 2013 revealed a typical male-philopatric and female-dispersal society. This pattern did not differ according to whether data were collected before or after the interruptions in our research or to the abandonment of artificial provisioning.

Thus, questions about why female bonobos transfer between unit groups and males remain in their natal group arise. As mentioned in the Introduction, there may be several reasons for this pattern, including the avoidance of inbreeding (Itani 1972; Pusey 1987; Clutton-Brock 1989), competition for local resources (Clark 1978;

Greenwood 1980; Waser 1985), and competition for local mates (Hamilton 1967; Dobson 1982; Moore and Ali 1984). The need for cooperation among kin may also be important in this regard (Perrin and Lehmann 2001; Le Galliard et al. 2006).

Intragroup Competition and Kin Cooperation

In one exceptional case involving chimpanzees at Mahale, four females remained in their natal group without transferring during a period in which the size of the study group decreased by half. Although the reasons for this behavior remain unknown, it suggests that the lower density reduced the competition for local resources or intragroup feeding and increased the benefits of remaining in the natal group. Because some adult males also disappeared during this period, the inbreeding risk or the possibility of father–daughter and sister–half-brother incest also decreased (Nishida et al. 2003; Nishida 2012). In contrast, the consistent tendency of females in the E1 group at Wamba to transfer, which has been evident since 2003, when the E1 group substantially expanded its home range (Tashiro et al. 2007; Idani et al. 2008), suggests that competition over local resources was not an important contributor to the transfer of female bonobos between unit groups. The lower population density seemed to reduce the intragroup feeding competition in the E1 group even after some remnants of the extinct groups were integrated into that group, which had occurred by 2006.

Competition for local mates (Hamilton 1967; Dobson 1982; Moore and Ali 1984) is also an unlikely explanation of the dispersal of female bonobos. Males that live in one-male units must encounter a high level of competition for local mates, but several species exhibit female-biased dispersal (e.g., hamadryas baboons, gorillas). Bonobos live in multi-male, multi-female groups, and it is assumed that there is less competition for local mates among males. Moreover, the prolonged sexual swelling of female bonobos would be expected to reduce the competition among males for mates (Thompson-Handler et al. 1984; Furuichi 1987; Kano 1992). Females are able to find mates in their natal group, although the possibility of father–daughter and sister–half-brother incest remains. The absence of second transfer by parous females indicates low intragroup competition among females for mates.

The issue of whether cooperation among male kin functions to protect females in estrus and/or mothers and offspring remains controversial with regard to bonobos. On the one hand, bonobos show tolerance for members of neighboring groups; although males are more aggressive than are females in intergroup encounters, copulation between members of different groups occurs (Idani 1990; our unpublished data). On the other hand, one genetic study showed that dominant males achieved high levels of success with regard to paternity, but issues related to extra-group paternity remain unclear (Gerloff et al. 2011).

If female bonobos remain in their natal groups, they may benefit from cooperating with kin, such as mother and sisters. However, the need for kin cooperation does not seem to prevent them from transferring between unit groups, because

they succeed in establishing cooperative bonds with unrelated females. The close associations and intimate bonding among females are key elements of bonobo society; that is, the less agonistic temperament of males, their priority of access to the food of females, the absence of infanticide, and intergroup tolerance (Nishida and Hiraiwa-Hasegawa 1987; Kano 1992; White 1996; White and Wood 2007; Furuichi 2011) are advantageous to female bonobos. Therefore, female bonobos are unlikely to pay extra costs for leaving their kin in their natal group or for unstable and risky social relationships with the resident individuals in a new group.

Avoidance of Inbreeding

The traditional view of inbreeding avoidance (Itani 1972; Pusey 1987; Clutton-Brock 1989) may explain part of the evolutionary basis of female transfer. However, as discussed in detail in Chap. 9, inbreeding in the natal group is not necessarily associated with serious disadvantages, especially when the inbreeding involves half-siblings. Additional research regarding the proximate causes of emigration and the mate choices by females in natal and new groups is needed to examine how inbreeding avoidance leads females to leave their natal groups.

One significant risk associated with remaining in one's natal group may be mother-son and father-daughter incest. The former would be less risky because both a mother and her son recognize their kin relationship and avoid incest (Kano 1992). The latter is more risky among bonobos, because paternity is ambiguous due to promiscuous mating patterns. The emigration of young females from their natal group reduces the possibility of father-daughter incest in a male-residence society.

Male bonobos remain in their natal group until the end of their life despite the low level of male bonding. We sometimes observed that adult males ranged alone for a month or more, but they ultimately returned to their original group (our unpublished data). For example, an adult male, Tawashi, had not been observed in the E1 group for about 5 months, from August 2008 to January 2009. During this time, villagers sometimes saw and heard a lone bonobo in the forest and near the crop fields. Tawashi seemed to have lived alone in the range of the E1 group. Males live alone for a variety of reasons. In the case of Tawashi, he lost the position of alpha male before his disappearance. After his return, he had clearly lost his previous vigor and vitality and may have contracted a disease. Despite the occurrence of such temporary disappearances, we have no records of unknown males entering or approaching the periphery of the E1 group, which suggests a strong tendency toward male philopatry.

In contrast to chimpanzees, male bonobos do not ally with other males in agonistic interactions. Therefore, male residence would not be needed to promote male bonding. Instead, lifelong mother-son bonding, which is a characteristic of bonobos, may be among the factors promoting male residence, because this pattern may offer benefits to both mothers and sons (Kano 1992; Furuichi 1997; Surbeck et al. 2011). The absence of a second transfer by parous females may support this notion. However, no evidence of intergroup transfer by orphan males is available.

In conclusion, bonobos show a strong tendency toward male philopatry and female dispersal despite the rarity of male bonding and the frequency of intimate female bonding. It is unlikely that intragroup competition for food and mates explains this tendency. Although future studies on issues such as extra-group paternity and mate choices by females are needed, cooperation among male kin, a relic of the common ancestry of bonobos and chimpanzees (Furuichi and Ihobe 1994), may be advantageous when male kin cooperate to protect relatively scattered females. Therefore, male residence and the risk of father–daughter incest may encourage female transfer in bonobos. Based on this tendency, females would have developed tactics to promote close association and intimate bonding with nonrelatives and to reduce the cost of male aggression. Female transfer at a young age may promote smooth integration into a new group and reduce the cost of transfer via frequent engagement in social play. Frequent social play would be also related to other paedomorphic characteristics of bonobos (e.g., the ventral position of female genitals, which enables GG rubbing between females) and to the high tolerance for other individuals (e.g., mother–son bonds) (Shea 1983; Kuroda 1989). It is intriguing that a type of social structure that differs from that of chimpanzees has developed in societies that show a consistent tendency toward female dispersal.

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