

Longitudinal Structure of a Unit-group of Bonobos: Male Philopatry and Possible Fusion of Unit-groups

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Introduction

Bonobos and chimpanzees have a male-philopatric social structure (Nishida 1979, Itani 1985, Goodall 1986, Wrangham 1986, Pusey and Packer 1987, Kano 1992, Wallis 1997, Reynolds 2005, Furuichi 2006). Demographic data from long-term research sites show that all males remain in their natal groups throughout life, while most females leave their natal groups and join neighboring groups. Itani (1977, 1985) argued that female or male philopatry is a rigid, species-specific social structure. However, some researchers have reported cases in which male chimpanzees or bonobos joined non-natal groups (Nishida and Hiraiwa-Hasegawa 1985, Sugiyama 1999, 2004, Hohmann 2001). Thus, it is not clear how consistent male philopatry is in chimpanzees and bonobos, and under which circumstances male transfer occurs in these species.

We have been conducting research on wild bonobos at Wamba since 1974 and have studied various aspects of bonobo ecology and behavior. Since the original identification of all members of the main bonobo study group in 1976, all natal females have disappeared before maturity, and no males have immigrated into the study group (Furuichi 1989); thus, we had been confident that male philopatry was a rigid social structure for wild bonobos.

Our long-term research was interrupted by political disorder in 1991. When we resumed research in 1994, we found that some individuals of our study group had disappeared (Furuichi et al. 1998). In 1996, our research was again interrupted by civil war. When we visited Wamba to observe security conditions in 2002 during a ceasefire, we confirmed that the main study group, E1, had survived the war (Furuichi and Mwanza 2003).

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Although some adult individuals of E1 disappeared during the wars, the total number of bonobos in E1 did not decrease (20 individuals in 1996; 25 individuals in 2004–2005). To our surprise, the number of adult males in E1 was larger than expected, even if we assumed that all of the immature males present before the wars had survived. This data meant that at least some adult males had joined E1 by individual transfer or by fusion of groups.

We re-examined the tendencies of male philopatry and female transfer in wild bonobos using data from E1 spanning 30 years. Furthermore, via direct observation and DNA analysis, we explored the nature of the increase in number of males that occurred in E1 during the wars.

Methodology

Study Site and Group

Our study site is at Wamba, in the northern sector of the Luo Reserve, Democratic Republic of Congo (Kano 1992, Hashimoto and Furuichi 2001, Idani et al. 2008). The Wamba research camp is located at 0°11'08"N, 22°37'58"E (WGS1984). The northern sector contains five settlements, where vegetation is comprised of primary forest, old secondary forest, young secondary forest, swamp forest, and agricultural fields (Kano 1992, Idani et al. 1994, Hashimoto et al. 1998). Bonobos use all five types of vegetation. Until 1996, when our research was interrupted, six unit-groups (E1, E2, Bokela, Plantation, Kofola, and Sema) had been using the northern sector as their entire home range or as a part of their home range (Kuroda 1979, Idani 1990, Kano 1992). The history of the Luo Reserve is described by Kano et al. (1996), Hashimoto & Furuichi (2001), Furuichi & Mwanza (2003), and Idani et al. (2008).

In 1976, researchers identified all members of the main study group, E. Two subgroups of E were present from the beginning of the study, and they split into independent groups (E1 and E2) in about 1983 (Kuroda 1979, Kano 1982, Furuichi, 1989, Kano 1992, Furuichi et al. 1998). The main focus of our study is E1, which had been artificially provisioned for a part of each year until 1996 (Kuroda 1979, Hashimoto et al. 1998), after which the study was interrupted by civil wars. We resumed study of the E1 in 2003 with no provisioning.

Observations

From 1974 to 1996, we observed E and then E1. After security conditions improved, our local assistants resumed observation of E1 in 2002. We resumed observation in August 2003, and thereafter two or more Japanese or Congolese researchers observed E1 continuously until January 2006. Throughout this period, we followed

E1 from sleeping site to sleeping site for 6 days a week whenever possible. We recorded the names of bonobos within visual range. See Mulavwa et al. (2008) for the number of observation days and mean hours of observation per day.

Though we did not employ artificial provisioning after resumption of the study in 2002, bonobos of E1 were well habituated by local assistants by August 2003. In March to April 2004, two of us observed E1 for about one month and identified all of its members. We continued to identify members of E1 until January 2006.

DNA Analysis

In 1990 and 1994, we collected wadge samples (the fibrous residue of sugarcane spat out by bonobos after chewing) from all members of E1 except for some of the infants. We determined the sequence of the D-loop region of the mitochondrial DNA (Hashimoto et al. 1996). After resumption of the study in 2003, we collected fecal samples from most adult members in March to April 2004; we collected supplementary samples in January 2005.

We collected fresh feces samples from each individual during observation. We placed them in plastic tubes with silica gel and kept them at ambient temperature in the field. We used the QIAamp DNA Stool Mini Kit (QIAGEN) to extract genomic DNA from the samples. We amplified a segment of the D-loop region of mitochondrial DNA consisting of 416-base pairs via the polymerase chain reaction (PCR) with the primers 5'-TAAAC TATTC TCTGT TCTTT CA-3' and 5'-CGGGA TATTG ATTTT ACGGA GG-3'. We conducted PCR via the Expand High Fidelity PCR System (Roche) in a GeneAmp PCR System 9700 (ABI) as follows: 4 min at 94 °C, 35 cycles of 30sec at 94 °C, 1 min at 47 °C, 2 min at 72 °C; and 10min at 72 °C; hold at 4°C. We checked the product by gel electrophoresis via CYBR Green (TAKARA). We collected the target band and conducted a second PCR with the same set of primers, according to the same protocol with the exception that we used 40 cycles rather than 35. We labeled the products via the BigDye Terminator v1.1 Cycle Sequencing Kit (ABI) and sequenced them with an ABI PRISM 310 Genetic Analyzer (ABI). We aligned sequences via Genetyx ver 5.0.

Results

Male Philopatry and Female Transfer

We list the males that we confirmed as members of E or E1 by 1996 in Table 5.1. We excluded members of E that belonged to E2 after group fission, because only individuals that belonged to E1 are included in this study. Ten males were present in E when all of the members were identified in 1976, and 11 males were born into

Table 5.1 Life history of males of E1 up to 1996

Name	Birth year	Immigration		Disappearance		Supposed cause
		Year	Age	Year	Age	
Kake	Initial member in 1976			1989	39–44	Death by old age
Kuro	Initial member in 1976			1991–92	36–42	Death by old age
Hata	Initial member in 1976			1991	31–36	Death by old age
Ika	Initial member in 1976			–		
Ibo	Initial member in 1976			1905/6/9	25	?
Mon	Initial member in 1976			–		
Tawashi	Initial member in 1976			–		
Goro	Initial member in 1976			1905/6/6		Death by poaching
Mitsuo	Initial member in 1976			1991–92	16–17	?
Ten	Initial member in 1976			–		
Haluo	1977			1989	12	?
Senta	1980			1992–94	12–14	?
Haku	1982			2002		Death by poaching
Matsu	1984			1988–89	4–5	Death in immature age
Hayato	1986			–		
Mao	1986			–		
Shijimi	1988			–		
Kikuo	1988			–		
Bio	1990			–		
Haze	1990			–		
Maro	1990			1995–1996	5–6	Death in immature age

E or E1 after 1976. No males immigrated from other groups to become permanent members of either E or E1.

Ten of the 21 males had died or disappeared by 1996. Six males (*Kake*, *Kuro*, *Hata*, *Goro*, *Matsu*, and *Maro*) are known to or are presumed to have died. We were unable to determine whether the other 4 males (*Ibo*, *Mitsuo*, *Haluo*, and *Senta*), whose ages ranged from 12 to 26 years, had died or emigrated. Since they were not observed in groups neighboring E1, and no case of immigration of adult males is confirmed for E1 or neighboring groups, they probably died.

We list the females that were confirmed as members of E or E1 by 1996 in Table 5.2. Eight females were present in E when we identified all members in 1976, and 15 females were born into E or E1 after 1976. Five additional females immigrated into E or E1 and became permanent members. Some other females visited E1 for a short period and then left; they are not included in Table 5.2. Nineteen of the 28 females had died or disappeared by 1996. Seven females (*Kame*, *Sen*, *Mitsu*, *Kameko*, *Naomi*, *Nako*, and *Midori*) are known to or are presumed to have died.

We could not determine whether the other 12 females had died or emigrated. Their ages ranged from 2 to 36 years, with a peak range of 6 to 10 years. Because at 6 to 10 years of age they were in good health and exhibited a tendency to stay on the periphery of the group when last observed in E1, they probably emigrated. The ages

Table 5.2 Life history of females of E1 up to 1996

Name	Birth year	Immigration		Disappearance		Supposed cause
		Year	Age	Year	Age	
Kame	Initial member in 1976			1990	40–45	Death by old age
Sen	Initial member in 1976			1992–94	42–47	Death by old age
Mitsu	Initial member in 1976			1992–94	37–42	Death by old age
Halu	Initial member in 1976					
Shiro	Initial member in 1976			1991–92	34–35	?
Bihi		1978	14			
Mayu	Initial member in 1976			1995–96	29–30	?
Nao		1983	12			
Miso		1984	10			
Kiku		1984	10			
Shin		1992–96	10–14			
Iku	Initial member in 1976			1980–81	9–10	?
Junko	Initial member in 1976			1980–81	9–10	?
Shiko	1978			1987	9	?
Kameko	1980			1981	1	Death in immature age
Biko	1981			1989	8	?
Mako	1981			1988	7	?
Balu	1982			1988	6	?
Toshi	1984			1992–94	8–10	?
Naomi	1985			1985	0	Death in immature age
Bibi	1986			1992–94	6–8	?
Miki	1986			1992–94	6–8	?
Nasa	1987			1995–96	8–9	?
Miho	1990			1992	2	Death in immature age
Nako	1993			1995	2	Death in immature age
Midori	1993					
Kino	1994					
Bina	1996					

of disappearance from and immigration into E1 differed (6–10 and 10–14 years, respectively), suggesting that, after leaving their home group, females visit several groups before finally settling in a new group. In fact, some young females of ca. 8–10 years of age visited E1 for a brief period and then left. Because we have observed no case of female transfer in this age class, it is assumed that the 2 females that disappeared in prime adulthood (*Shiro* and *Mayu*) probably died. Some females with dependent offspring visited E1, but they eventually returned to their original groups.

A comparison by sex of the ages of appearance and disappearance from E1 is in Fig. 5.1. The appearance of males exclusively occurred only at birth. The appearance of females, except for births, exclusively occurred at the age of 10–15 years. In contrast, disappearance was extremely frequent among females 5–10 years old. This comparison supports the supposition that only females transfer between unit-groups in wild bonobos, whereas males remain in their natal groups.

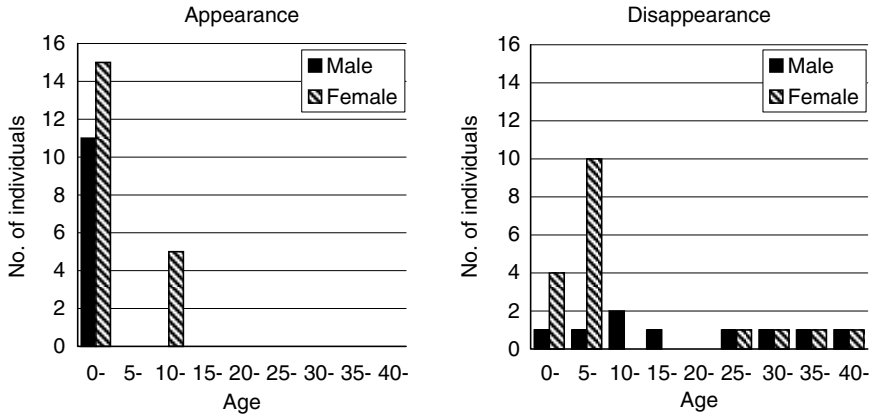


Fig. 5.1 A comparison by sex of the ages of appearance in and disappearance from E and E1. Appearances in the age class 0–5 are births.

Disappearance of Neighboring Groups and Possible Fusion of Unit-Groups

During our absence, the number of E1 group members decreased from 20 in 1996 to 17 in 2004 (Fig. 5.2). Our local assistants reported that soldiers killed a young adult male of E1, *Haku*, and that other cases of hunting by soldiers or local people might have occurred. Moreover, many adult individuals had new injuries, such as loss of digits, which appeared to be caused by wire snares set for bush pig or antelope. Some bonobos, especially young individuals, may have been killed by such injuries.

Bonobo deaths from hunting may have occurred less frequently in E1 than in other groups because E1 occupied the interior of the reserve, whereas the other groups occupied the periphery. Deaths from human activities likely caused the disappearance of some peripheral groups during our absence.

In 1991, prior to which year the political situation had been stable, six groups claimed home ranges in the northern sector of the Luo Reserve (Fig. 5.3). From direct observation of them, we estimated that the total number of bonobos was about 250. However, the number of bonobos decreased by half between 1991 and 1996, probably as a result of increased poaching during our absence between 1991 and 1994. In 2005, we observed only 3 of the 6 groups, E1, E2, and Plantation. Two other groups, Kofola and Bokela, probably disappeared due to poaching, given that we walked in their home ranges many times and found no trace of them. The presence of another group, Sema, is unclear because we visited their home range infrequently (Fig. 5.3).

During our absence from 1996 to 2003, E1 greatly extended their home range to the east and northeast, areas previously used by Bokela and Kofola (Fig. 5.4). In 2004, 6 individuals appeared to join E1 when E1 visited the area. We first observed *Nord*, *Yuki*, *Jacky*, and their infants in April 2004 in the eastern part of the E1 home

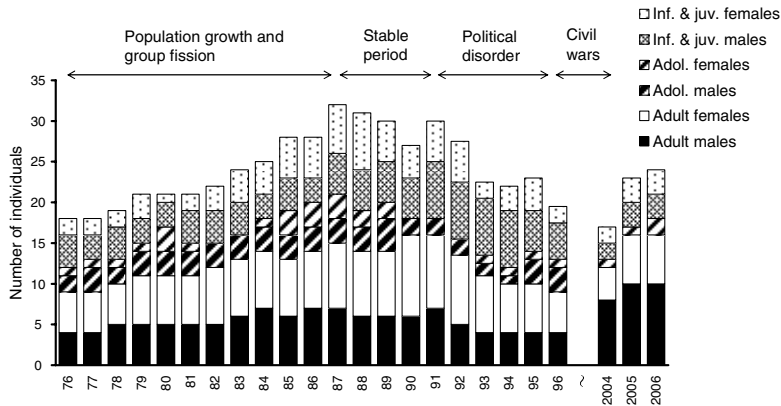


Fig. 5.2 Demographic changes of E1. E1 split from the E group in or around 1983. Bars before 1982 indicate individuals in the southern subgroup of E1 that eventually became the independent E1 group.

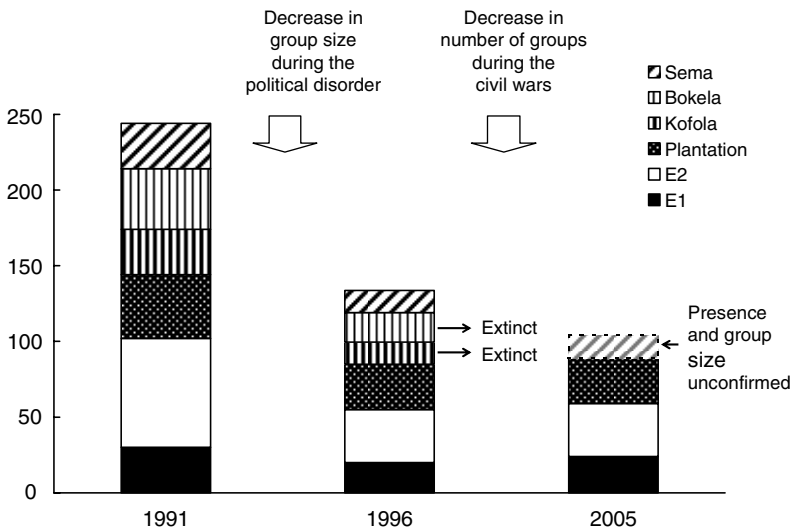


Fig. 5.3 Changes in the estimated number of bonobos in the northern sector of the Luo Reserve.

range. They were all shy toward human observers, and they did not follow E1 members when they left the area for the western part of their home range. After September 2004, they became regular members of E1, and they ranged together even in the western area. We first observed *Dai* in E1 in September 2004 when E1 visited the eastern area. He was shy and avoided human observers. From November 2004, he became a more regular member of E1 and became accustomed to human observers.

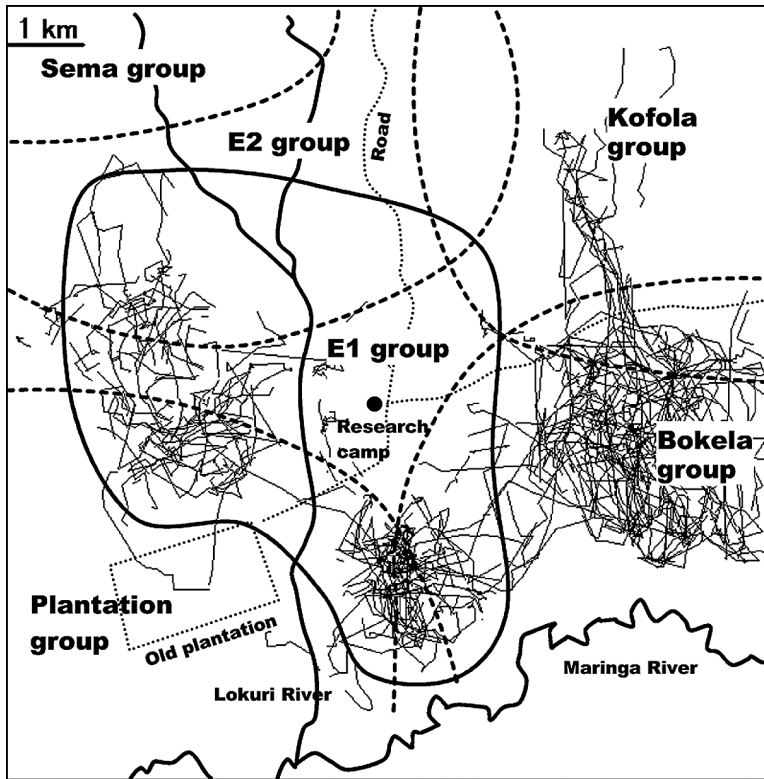


Fig. 5.4 Ranging routes of E1 and vegetation of the ranging area. Each jagged line denotes a ranging route from one tracking session. The vegetation was mapped from Landsat data recorded on January 14, 1991 (Hashimoto et al., 1998).

Re-Identification of E1 Members

Before our research was interrupted in 1996, we had identified 20 individuals (4 adult males, 6 adult females, and 10 immature individuals) in E1 (Table 5.3). After research resumed in 2003, we identified 24 individuals (10 adult males, 7 adult females, and 7 immature individuals). In 2004, we identified 2 of the adult males, *Ten* and *Tawashi*, by external characteristics, and we assumed the other 8 adult males (*Gausche*, *Mori*, *Noire*, *Nobita*, *Loboko*, *Jeudi*, *Nord*, and *Dai*) to be individuals that had been immature males with no conspicuous traits in 1996. Of the 7 immature males in 1996, one (*Haku*) was killed during the civil war. Therefore, in 2003, 6 males (*Hayato*, *Mao*, *Shijimi*, *Kikuo*, *Bio*, and *Haze*) may have still been present in E1; they were candidates for the newly named 8 adult males.

To confirm their identity, we analyzed mitochondrial DNA sequences from fecal samples. We matched 4 of the newly named 8 adult males to 4 immature males of 1996. The sequence of *Noire* matched that of *Mayu*, who is the mother of *Mao*.

Table 5.3 Members of the E1 group in 1996 and in 2004–2006

Sex	Members in 1996		Members in 2004–2006		Possible identity suggested by DNA sequence and other traits
	Name	Age in years in Jan 1996	Name	Age in years in Jan 2005	
Male	Ika	34–36*			
	Mon	29*			
	Tawashi	22*	Tawashi	29*	
	Ten	26*	Ten	35*	
	Haku	13			
	Hayato	9	(Hayato)	(18)	
	Mao	9	(Mao)	(18)	
	Shijimi	7	(Shijimi)	(16)	
	Kikuo	7	(Kikuo)	(16)	
	Bio	5	(Bio)	(14)	
	Haze	5	(Haze)	(14)	
			Gauche	15–19*	
			Nord	20*	
			Dai	30*	
			Mori	9–14*	Mori or Jeudi is probably identical to Bio
			Noire	15–19*	Probably identical to Mao
			Nobita	15–19*	Probably identical to Kikuo
			Loboko	9–14*	
			Jeudi	9–14*	Mori or Jeudi is probably identical to Bio
			Jiro	3–4*	
		Kitaro	0		
		Shiba	0		
		Hokuto	Died at 2 years old in 2004		
Female	Halu	39*			
	Bihi	32*			
	Nao	25*	Nao	34*	
	Miso	22*			
	Kiku	22*	Kiku	31*	
	Shin	14*	(Shin)	(23*)	
	Midori	2			
	Kino	1			
	Bina	0			
			Hoshi	20–24*	Remains a possibility that Hoshi is Shin
			Sala	13–14*	
			Yuki	20–24*	
			Jacky	15–19*	
			Moseka	10*	
			Kirara	7*	
			Nana	4*	
		Yukiko	2–3*		
		Nachi	0		

* Age estimated. Names and ages in parentheses for members in 2004–2006 shows the individuals who might be existing but identified with different names.

The sequence of *Nobita* matched that of *Kiku*, who is the mother of *Kikuo*. No individuals present in 1996 had mothers whose sequence matched those of *Mayu* or *Kiku*, except for *Mao* and *Kikuo*. Therefore, *Noire* and *Mao* are likely the same individual, as are *Nobita* and *Kikuo*. The sequences of *Mori* and *Jeudi* are identical to that of *Bihi*, the mother of *Bio*. However, *Bihi* had only one son, *Bio*, in 1996, and no adult female in 1996 had a sequence that matched that of *Bihi*. Therefore, either *Mori* or *Jeudi* is likely to be the same individual as *Bio*. The other male probably joined E1 during or after the war.

We did not analyze the DNA of 4 adult males (*Gausche*, *Loboko*, *Nord*, and *Dai*) because of a lack of samples. If they were previously immature members of the 1996 E1 group, 3 of them might be *Hayato*, *Shijimi*, or *Haze*, and the fourth might be an immigrant into E1. Therefore, at least two males (either *Jeudi* or *Mori* and either *Gausche*, *Loboko*, *Nord*, or *Dai*) seem to have entered E1 during or after the war.

Discussion

Like chimpanzees, bonobos have a male-philopatric social structure. Males remain in their natal unit-group, whereas females leave their natal unit-group before sexual maturity and transfer between groups (Wrangham 1986, Kano 1992, Furuichi, 2006). In our study group, E and E1, no cases of male transfer were observed between 1976 and 1996, though there were many cases of female emigration and immigration during the same period (Furuichi 1989, Kano 1992, this study). However, after an interruption of the study from 1996 to 2002, at least two males joined E1 from other groups.

In early studies of primate social systems, Itani (1977, 1985) argued that each primate species has a specific basic social structure that is strongly affected by its phylogenetic position, and male or female philopatry is a basis for primate social structures. In general, this claim is still valid, but there are some exceptional cases of transfer by males or females. For example, some researchers reported temporary visits of out-group males in male-philopatric unit-groups of bonobos and chimpanzees. Hohmann (2001) reported that 2 strange adult males visited and stayed in his bonobo study group at Lomako for 12 months, and that one of them developed friendly social relationships with resident males. In addition, one juvenile male chimpanzee at Mahale encountered members of another group when his mother temporarily joined the M group (Nishida and Hiraiwa-Hasegawa 1985). At Bossou, 2 strange adult male chimpanzees joined a semi-isolated group of chimpanzees and stayed there for several days, and another adult male joined and stayed for several months (Sugiyama 1999). Moreover, most adolescent and young adult males disappeared from Bossou, and at least some of them must have emigrated (Sugiyama, 2004).

Three cases of female transfer have been reported for Japanese monkeys, which have a matrilineal social structure. Takahata et al. (1994) reported that 2 females transferred to an adjacent troop when their troop rapidly decreased in size, leaving

them as the last 2 surviving members. Sugiura et al. (2002) also reported 2 cases of transfer of a female when she became the last member of a declining troop.

Gibbons have monogamous social groups in which both males and females leave their natal groups and form new ones without joining other groups. However, a young adult male and a young adult female joined non-natal monogamous groups and settled there after their forested habitat was fragmented by forest fire (Oka & Takenaka 2001).

Since most of the cases described above occurred under unusual circumstances, immigration of the strange males to E1 in our study might have also occurred under these circumstances. When we resumed research on E1, we found that their home range had expanded into the eastern area previously used by the Kofola and Bokela groups, probably because the disappearance of these groups left their home ranges vacant. When we first observed *Nord*, *Yuki* and her infant, and *Jacky* and her infant in E1, the group was ranging in the eastern area. Even after they joined E1, for several months they remained in the eastern area when the main members of E1 went back to the west. We also first observed *Dai* when E1 was ranging in the eastern area. Not only immigration of males, but also that of females with infants was unusual. We observed no permanent immigration of adult females with infants in the first 20 years of study of E and E1. Thus, this case might be better understood as aggregation of declining groups, rather than a strict intergroup transfer of adult males. Exactly what caused the immigration of *Jeudy* or *Mori* in our absence during the war is unclear. However, it is possible that something similarly unusual happened when the local population of bonobos was severely impacted by human activities.

Although some cases of male transfer have been reported in chimpanzees, there is no record of permanent immigration of adult males. This fact may reflect the intolerant relationships between males from different groups of chimpanzees (Nishida 1985, Goodall 1986, Wrangham and Peterson 1996, Reynolds 2005). Contrarily, bonobos sometimes display affiliative relationships between different groups (Idani 1990). Different groups of bonobos sometimes forage together for as long as a week, and members of these groups exhibit affiliative social interactions. Though further observation of the new immigrants is needed, the high tolerance between different groups of bonobos might have enabled the permanent aggregation of fragmented groups, as observed in the above-mentioned cases of Japanese macaques.

Acknowledgments We thank Drs. Takayoshi Kano and Toshisada Nishida for their continued support of the study at Wamba and for research guidance. We also thank Dr. Tetsuro Matsuzawa and Ms. Sally Coxe for aiding resumption of the study; Drs. Shin Nakamura and Akiko Takenaka for their support of our laboratory work; Dr. Mwanza and members of the Research Center for Ecology and Forestry (CREF) of the Democratic Republic of Congo for their support of our field work; and Dr. Shigeo Uehara and members of the Primate Research Institute, Kyoto University, for valuable discussion and advice. We are grateful to Mr. Nkoi Batolumbo and other local staff and villagers for their support during and after the war. This study was supported by the National Geographic Fund for Research and Exploration (#7511-03 to Furuichi), the JSPS core-to-core program HOPE (#15001 to Matsuzawa), JSPS Grant-in-Aid for Scientific Research (#17570193 to Hashimoto, #12575017 and 17255005 to Furuichi), and Japan Ministry of Environment Global Environment Research Fund (#F-061).

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