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ORIGINAL ARTICLE

Do immigrant female bonobos prefer older resident females as important partners when integrating into a new group?

Kazuya Toda[1] · **Takeshi Furuichi**[1]

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Abstract

Intergroup transfer is a critical part of the life history of group-living species, with considerable variation in its timings and patterns among species. Immigrant female bonobos are documented to smoothly integrate into a new group through forming affiliative relationships with old, high-ranking resident females (Idani, Folia Primatol 57:83–95, 1991). However, only a few studies are available on immigration costs and strategies for female bonobos. Here, we compared social relationships of natal females (known to be 4.5–7.2 years old) and immigrant females (estimated to be 6.8–12.3 years old) from one bonobo group at Wamba in the Luo Scientific Reserve, Democratic Republic of the Congo. Similar to previous studies, resident females did not appear to spatially isolate immigrant females or act aggressively toward them. However, resident males were more frequently aggressive toward immigrant females than toward natal females. Both natal and immigrant females tended to groom high-ranking females more than middle- and low-ranking females, although immigrant females spent more time grooming unrelated females than natal females. Immigrant females did not exhibit rank-related partner preference for genito-genital rubbing and copulation. Although we did not control for age differences because of the small sample size, our results provide partial support for the hypothesis that old female bonobos are important partners for the successful integration of young females into an unfamiliar group. This strategy could explain why female bonobos disperse before reaching sexual maturity, which contrasts with the need for female chimpanzees to display sexual swellings and draw male interest as protection against aggression from resident females.

Keywords *Pan paniscus* · Female transfer · Social integration · Partner preference · Codominance hierarchy · Wamba

Introduction

In the life history of group-living animals, intergroup transfer or social dispersal is a key event involving emigration from a familiar group and immigration into an unfamiliar group (Isbell and Van Vuren 1996). Dispersal from the natal group brings future fitness benefits through the avoidance of inbreeding depression (Pusey and Wolf 1996) and intragroup competition for limited resources (Moore and Ali 1984). However, dispersal often incurs potential fitness costs, including greater predation risk, reduced feeding efficiency, and social stress (Isbell et al. 1993; Pinter-Wollman et al. 2009; Maag et al. 2019). Furthermore, mammalian females generally invest more in their offspring than males. The high cost of gestation and infant care is a potential factor driving females to avoid dispersal and encouraging them to maintain long-term cooperation with kin in natal groups (Clutton-Brock and Lukas 2012). Consequently, male-biased transfer is relatively more prevalent among group-living mammals (Greenwood 1980; Pusey and Packer 1987), although female-biased transfer exists in some primate taxa (Moore 1984; Lee and Strier 2015).

Bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) diverged approximately 1.0 million years ago (Takemoto et al. 2015). Both species live in multi-male and multi-female groups where males typically remain in the natal group while nulliparous females transfer between groups (Nishida and Kawanaka 1972; Pusey 1979; Kano 1982). Long-term field studies have demonstrated that female bonobos leave the natal group at an earlier age [around 6–8 years old (Sakamaki et al. 2015; Lee et al. 2020)] than female chimpanzees do [around 11–13 years old (Stumpf et al. 2009; Nakamura 2015; Walker et al. 2018; Wittig and

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✉ Kazuya Toda
toda.kazuya.h17@kyoto-u.jp

[1] Primate Research Institute, Kyoto University, Kanrin 41, Inuyama, Aichi 484-8506, Japan

Boesch 2019)]. Additionally, female chimpanzees often exhibit sexual swellings of the perineum and begin copulating with mature males before dispersal (Pusey 1990; Nishida et al. 2003). In contrast, female bonobos remain sexually immature, with no adult-like perineal swelling, and seldom copulate with mature males before dispersal (Hashimoto 1997; Sakamaki et al. 2015). This difference in the female developmental stage during dispersal might be related to the social relationships formed as females immigrate into a new group.

Resident females may attempt to prevent the entry of new females when the socio-ecological costs of intragroup competition exceed the benefits of large groups (Sterck et al. 1997; Koenig 2002). Aggression toward immigrant females is present in some primate species, although the degree is variable between and even within species [e.g., chimpanzees (Nishida 1989; Boesch and Boesch-Achermann 2000; Townsend et al. 2007; Kahlenberg et al. 2008b; Pusey et al. 2008); mountain gorillas (*Gorilla beringei*) (Watts 1991); ursine colobus (*Colobus vellerosus*) (Teichroeb et al. 2009); red howlers (*Alouatta seniculus*) (Crockett and Pope 1988); mantled howlers (*Alouatta palliata*) (Glander 1992); Geoffroy's spider monkeys (*Ateles geoffroyi*) (Riveros et al. 2017); northern muriquis (*Brachyteles hypoxanthus*) (Printes and Strier 1999)]. While these actions toward immigrant females are mostly threat behaviors, harassment can escalate into severe attacks. As a result, new immigrant females may have a lower feeding efficiency than natal females, leading to delayed onset of their first parturition [e.g., chimpanzees (Kahlenberg et al. 2008b; Walker et al. 2018)]. However, female bonobos, especially old females, are unique in their high tolerance toward immigrant females (Idani 1991; Sakamaki et al. 2015; Toda and Furuichi 2020). This lack of aggression may be related to the observation that female bonobos participate in a wide range of affiliative and cooperative relationships regardless of kinship (Tokuyama and Furuichi 2016; Moscovice et al. 2017).

In contrast to females, resident males have a greater investment in acquiring outgroup females because male reproductive opportunities (and hence fitness) increase with more females in a group (Steenbeek 1999; Sicotte 2002). Thus, resident males may physically intervene when resident females act aggressively toward immigrant females [e.g., chimpanzees (Nishida 1989; Boesch and Boesch-Achermann 2000; Kahlenberg et al. 2008a); mountain gorillas (Watts 1991, 1992)]. The social passport hypothesis thus suggests that female chimpanzees advertise their sexual swellings to resident males when integrating into a group, functionally recruiting males as protectors (Nishida 1989; Kahlenberg et al. 2008a). However, female bonobos do not appear to attract resident males during dispersal (Sakamaki et al. 2015). Instead, they focus on forming bonds with old resident females (Idani 1991), who play a central role in foraging and collective movement (e.g., Parish 1996; Tokuyama and Furuichi 2017). Female bonobos are codominant with males, and old resident females are the highest ranked in the bonobo dominance hierarchy (Furuichi 1997), possibly making them effective partners for immigrant females seeking smooth integration. This dominance structure differs notably from that of chimpanzees, wherein all females are subordinate to adult males (Goodall 1986; Nishida 2003).

Although wild bonobos have been studied for more than 40 years, female immigration events are not well understood because they rarely occur. Thus, this study aimed to investigate the immigration strategies of female bonobos. We compared the social interactions and spatial relationships of nulliparous natal and immigrant females with long-term resident females and males in one group of wild bonobos. We used these data to test four predictions derived from Idani (1991): compared with natal females, immigrant females experience a similar or lower amount of aggression from resident females; compared with natal females, immigrant females are closely associated with resident females at a similar or higher rate; immigrant females groom high-ranking resident females more often than natal females do; immigrant females prioritize sexual interactions [i.e., genito-genital (GG) rubbing] with high-ranking resident females over natal females.

Methods

Study group and subjects

Data were collected from E1, a habituated group of wild bonobos at Wamba in the Luo Scientific Reserve, Democratic Republic of the Congo, where field research has been conducted since 1973 (Kano 1992; Furuichi et al. 2012). Artificial provisioning was initially used for behavioral observations, but this practice was halted in 1996 when field research was interrupted by civil war (Hashimoto et al. 2008). Observations of the E1 group resumed in 2003 under natural conditions (no provisioning) and have since been performed daily. Group membership experienced a major change during the research absence between 1996 and 2003, and by 2004, existing and new individuals were identified (Hashimoto et al. 2008). This study was conducted between November 2014 and June 2018 and included five different 3- to 6-month-long periods of data collection: November 2014–February 2015, July–October 2015, May–October 2016, February–July 2017, and February–June 2018. During the study period, the E1 group comprised 31–43 individuals, including from two to five adolescent females (nulliparous; 8–15 years old), nine to 12 adult females (parous; > 15 years old), three to five adolescent males (8–15 years old), and eight or nine adult males (> 15 years).

We collected behavioral data on all juvenile and adolescent females in the E1 group. In this study, we used data from five natal females (NF) sampled within 2 years before leaving the E1 group and four immigrant females (IF) within 2 years after joining this group (Table 1). Four IFs directly immigrated from their natal groups PE or PW via intergroup encounters. All members of the PE and PW groups have been known since 2011 and 2012, respectively (Sakamaki et al. 2018), meaning that IFs were already well habituated to observers at the start of this study. Age ranges were confirmed to be 4.5–7.2 years old for NFs and estimated at 6.8–12.3 years old for IFs. Despite individual differences in the development of sexual swellings, NFs were all categorized as immature before emigration (e.g., Figs. S1A, B), whereas IFs exhibited clear sexual swellings within 1 year after immigration (e.g., Fig. S1C, D). Adolescent/adult females ($n = 10$) and adolescent/adult males ($n = 11$) that had been part of the group for over 2 years at the start of this study were considered resident females (RF) and resident males (RM) (Table 2). All five NFs had RF mothers, but none had maternal RM brothers.

Behavioral observations

Bonobos exhibit fission–fusion grouping dynamics (Kuroda 1979; White 1988). Females were selected for continuous focal sampling in a predetermined random order, with each bout lasting for 30 min. A bout of focal sampling was terminated if we lost sight of the focal individual for more than 15 min. After a 5-min interval, the next focal subject was selected for a new bout of focal sampling. To ensure a degree of independence in the focal data, upon sampling a female once, at least 120 min were required to elapse before following the same female again. Subjects observed at lower frequencies due to fission–fusion grouping dynamics were prioritized for focal sampling.

We recorded feeding, resting, moving, playing, social grooming, and other social interactions (e.g., agonistic interactions, sexual interactions, and begging for food) within one focal bout. Participant identity for these social interactions was also noted. During focal follows, 5-min scan sampling (six scans per bout) was implemented to record neighbors of the focal female (group members within 5 m) and their activity (i.e., feeding, resting, moving, and grooming). Group members that were visible during a focal bout were noted as part of a focal party to control for variation in the time when the focal female and each resident member were co-present. In total, 275.6 h of focal data (30.6 ± 7.4 h per female; Table 1) were collected. Each focal bout averaged 25.9 ± 4.9 min and consisted of 5.2 ± 1.1 scan samples (3270 scans in total).

Agonistic interactions were recorded, including aggression type, context, and outcome. Aggressive behaviors

Table 1 Data on five natal females (*NFs*) and four immigrant females (*IFs*) from the E1 group at Wamba in the Luo Scientific Reserve, Democratic Republic of the Congo, between November 2014 and June 2018

Identity	Natal group	Birth	Age range (years old)	Mother	Immigration or emigration	Focal observation period [hours (number of sessions)]					
						First	Second	Third	Fourth	Fifth	Total
Natal female (NF)											
Nadir	E1	September 2008	6.2–7.0	Nova	September 2015	15.4 (34)	5.0 (12)				20.3 (46)
Natsuko	E1	May 2009	5.5–6.5	Nao	November 2015	16.4 (36)	8.7 (24)				25.1 (60)
Yume	E1	October 2009	5.1–6.8	Yuki	August 2016	14.8 (33)	10.8 (27)	14.4 (32)			40.0 (92)
Otoko	E1	January 2011	4.5–6.5	Otomi	July 2017		11.9 (30)	13.5 (31)	14.6 (34)		40.0 (95)
Fua	E1	January 2011	5.3–7.2	Fuku	March 2018			13.4 (32)	16.7 (36)	3.1 (8)	33.2 (76)
Immigrant female (IF)											
Puffy	PE	Est. 2003–2005[a]	Est.10.3–12.3[b]	Pao	October 2013	12.4 (27)	10.5 (24)				22.9 (51)
Ichiko	PE	Est. 2007–2008[a]	Est.6.8–8.8[b]	Ichi	October 2014	14.7 (34)	11.3 (27)	11.0 (26)			37.0 (61)
Sachi	PE	Est. 2008–2009[a]	Est.6.8–8.5[b]	Sachi	November 2015		1.8 (4)	10.7 (25)	13.6 (30)		26.1 (59)
Debby	PW	Est. 2009[a]	Est.7.1–8.9[b]	Deko	August 2016			11.2 (26)	12.5 (30)	7.4 (18)	31.1 (74)

[a] Years if burtg was estimated (*Est.*) from physical features at the time of identification

[b] Age range was calculated based on the median of the estimated birth range

Table 2 Data on ten resident females (*RFs*) and 11 resident males (*RMs*) from the E1 group at Wamba in the Luo Scientific Reserve between November 2014 and June 2018

Identity	Birth	Immigration or group fusion	Dominance rank		
			David's score	Order within the same sex	Class within the same sex
Resident female (RF)					
Nao	Est. 1971	November 1983	20.7	3	High
Kiku	Est. 1974	December 1984	63.9	1	High
Hoshi	Est. 1981–1985	1996–2003[a]	19.4	4	High
Yuki	Est. 1981–1985	April 2004[a]	24.7	2	High
Jacky	Est. 1986–1990	April 2004[a]	10.9	6	Middle
Sala	Est. 1991–1992	1996–2003[a]	6.8	7	Middle
Nova	Est. 1994–1995	August 2007	16.2	5	Middle
Otomi	Est. 1997	June 2008	− 3.8	9	Low
Fuku	Est. 1998	April 2008	0.42	8	Low
Zina	Est. 2002	October 2011	− 24.5	10	Low
Resident male (RM)					
Ten	Est. 1970	(Native)	− 17.4	6	Middle
Tawashi	Est. 1974	(Native)	− 22.2	8	Low
Dai	Est. 1975	September 2004[a]	− 34.6	9	Low
Goche	Est. 1986–1990	1996–2003[a]	2.4	3	High
Nobita	Feb–Sep. 1988	(Native)	22.0	2	High
Jeudi	Est. 1991–1996	1996–2003[a]	− 3.7	4	Middle
Loboko	Est. 1991–1996	1996–2003[a]	− 21.0	7	Middle
Jiro	Est. 2001–2002	April 2004[a]	− 11.3	5	Middle
Kitaro	Feb. 2004	(Native)	72.1	1	High
Shiba	Nov. 2004	(Native)	− 35.4	10	Low
Joe	Oct. 2006	(Native)	− 87.5	11	Low

[a]Members that likely joined the E1 group because their original groups had been poached during the research absence between 1996 and 2003 (Hashimoto et al. 2008)

involved hitting, kicking, biting, pushing, chasing, charging, branch-dragging, and shaking branches. Submissive behaviors in response to aggression included fleeing, avoiding, grinning, screaming, and other submissive vocalizations. Other behaviors in response to aggression were retaliation toward the aggressor or intervention by a third party. These above behaviors were defined based on ethograms produced by Kano (1998) and Nishida et al. (1999). In addition, grooming interactions were recorded as the time spent grooming and being groomed. The duration of grooming/being groomed with each partner was separately recorded in the case of simultaneous mutual (bidirectional) grooming and polyadic grooming (involving three or more individuals) (Sakamaki 2013). Copulation and genital contact were recorded as sexual interactions. Copulation was defined as mounting and inserting the penis into the vagina, regardless of whether ejaculation occurred (Hashimoto 1997). Genital contact included GG rubbing, non-copulatory mounting, and rump-rump contact.

Assessment of dominance

The dominance hierarchy of the E1 group was determined from ad libitum observations of dyadic agonistic interactions involving ten RFs and 11 RMs. Across the study period, 39 instances of female intrasexual aggression, 395 instances of male intrasexual aggression, and 128 instances of intersexual aggression were recorded. David's scores (David 1987) were calculated for each RF and RM, based on dyadic dominance indices with the proportions of wins and losses corrected for chance, using the observed matrix of agonistic interactions (de Vries 1998). The sociomatrix included both sexes because female and male bonobos are codominant (Furuichi 1997; Surbeck and Hohmann 2013). A within-sex ranking (high, middle, and low) was created based on the obtained David's scores (Table 2). Dominance ranks were significantly correlated with age for RFs (Spearman's rank correlation test: $\rho = -0.82$, $p = 0.004$), but not for RMs ($\rho = -0.11$, $p = 0.738$).

Data analysis

All data were analyzed in R version 4.0.2 (R Core Team 2020). Significance was set at $p < 0.05$. We calculated frequencies of aggression to and from NFs/IFs and RFs/RMs. Dyadic dominance relationships between IFs and RFs/RMs, as well as between NFs and IFs, were described. Cases of RFs/RMs intervening in aggression against focal individuals were also reported.

The proximity of NFs/IFs with RFs/RMs (as a proportion of total scan time) during feeding on fruits and resting was compared using two separate generalized linear mixed models (GLMM) using the glmer function in the lme4 package (Bates et al. 2015). One scan sample was randomly resampled per focal bout to avoid spatiotemporal autocorrelation. The resampling procedure was applied to scan samples during feeding and resting periods. Each RF/RM located within 5 m of focal females was counted per scan (presence = 1, absence = 0) when it was present in the focal party to yield a proportion of scans as near neighbors. These proximity proportions were included as a response variable in models with a binomial error structure, using the cbind function (Baayen 2008). Our test predictors were the class of focal females (NF vs. IF), resident sex (RF vs. RM), and the class-sex interaction. Kinship with RFs (mother vs. other) was included as a covariate to control for its confounding effects. Subject (nine NF/IF individuals and 21 RF/RM individuals) was included as a random effect.

We also built four other GLMMs to examine whether NFs/IFs differed in their grooming and sexual interactions with higher-ranking RFs/RMs. Because each focal bout was 30 min, we constructed a binomial response variable of whether grooming and sexual interactions were present (1) or absent (0) during the focal bout. Our test predictors were the class of focal females (NF vs. IF), rank of RFs/RMs (high vs. middle; high vs. low), and the class-rank interaction. Kinship with RFs (mother vs. other) was included as a covariate in the grooming interaction model. Data on NFs and their mothers were removed from the sexual interaction model because such interactions never occurred during focal sampling. The identities of focal females (nine individuals) and RFs/RMs (ten and 11 individuals, respectively) were also included in each model as random terms.

We determined the significance of the interaction term in all binomial models by conducting a type II Wald test (Langsrud 2003) using the ANOVA function in the R car package (Fox and Weisberg 2019). If an interaction term was not significant, the model was refitted without the interaction but included test and control predictors as independent fixed effects. Through the anova function in the R stats package, likelihood ratio tests were used to compare full model fit with the respective null model that included control predictors (kinship) and random effects (Dobson and Bernett 2008).

The total duration of grooming interactions involving focal females was calculated for each sex and rank to investigate their reciprocal grooming relationships with RFs and RMs. Because kinship should affect the reciprocal grooming relationships, the duration of mother-daughter grooming was calculated separately from that of other pairs. Over 15 min of grooming data collected per rank and sex were used to calculate the reciprocity indices as follows: $(\Sigma \text{ receiving} - \Sigma \text{ giving})/(\Sigma \text{ receiving} + \Sigma \text{ giving})$. The index ranged from -1 (when focal females groomed but were not groomed at all) to 1 (when focal females were groomed but did not groom at all).

Results

The NFs and IFs did not significantly differ in the proportion of time they spent feeding (Mann–Whitney *U*-test: $W = 11$, $p = 0.903$), resting ($W = 13$, $p = 0.540$), moving ($W = 12$, $p = 0.713$), and social grooming ($W = 6$, $p = 0.391$) (Fig. 1). However, NFs spent more time playing than IFs ($W = 1$, $p = 0.037$), while the latter spent more time in social interactions, including agonistic interactions and sexual interactions ($W = 20$, $p = 0.020$).

Agonistic interactions

We observed 42 instances of aggression from other group members toward focal females (Table S1); these did not cause obvious injury. NFs and IFs received aggression at frequencies of 0.08–0.25 and 0.14–0.26 events/h, respectively; the difference was not significant (Mann–Whitney *U*-test: $W = 17$, $p = 0.11$). The percentage of aggression received during feeding was similar between NFs (52.6%) and IFs (52.1%). However, RMs were aggressive toward IFs more frequently than toward NFs ($W = 20$, $p = 0.018$), whereas RFs were equally aggressive toward both classes of focal females ($W = 9.5$, $p = 1.00$). Males that were aggressive toward focal females were not subsequently observed to copulate with them during the same focal bout. In three cases, RFs (Yuki, Nao, and Nova) drove away RMs (Nobita, Ten, and Kitaro) that displayed toward focal females (Nadir, Puffy, and Ichiko).

Focal females engaged in eight instances of aggression toward other group members (Table S1), initiating aggressive behaviors at frequencies of 0–0.08 (NFs) and 0–0.09 events/h (IFs). The frequency of aggression did not differ between NFs and IFs (Mann–Whitney *U*-test: $W = 19$, $p = 0.898$). Neither class exhibited aggressive behaviors toward RFs and RMs, except toward Joe, the youngest and lowest-ranking RM. One older IF (Puffy) chased him twice, and another NF (Otoko) hit him when he was copulating with her mother. IFs sometimes showed aggressive behaviors toward NFs, but NFs were not observed displaying aggressive behaviors toward IFs.

Table 3 Results from models testing the effects of focal female class, resident sex, and kinship on the proportion of scans where NFs and IFs were closely associated with each RF after non-significant interactions had been removed

Term	Estimate	SE	*Z*	*p*
Proximity with RF/RM when feeding on fruit				
(Intercept)	− 0.39	0.27	− 1.43	0.154
Class of focal female (NF vs. IF)	0.28	0.16	1.71	0.087
Sex of resident (RF vs. RM)	− 0.38	0.18	− 2.11	0.035*
Kinship (mother vs. other)	− 1.92	0.26	− 7.38	<0.001*
Proximity with RF/RM when resting				
(Intercept)	− 0.91	0.18	− 3.58	<0.001
Class of focal female (NF vs. IF)	− 0.22	0.20	− 1.13	0.259
Sex of resident (RF vs. RM)	− 0.54	0.19	− 2.90	0.004*
Kinship (mother vs. other)	− 1.52	0.19	− 7.89	<0.001*

For abbreviations, see Tables 1 and 2

* $p < 0.05$

Spatial relationships

The interaction of focal female class and resident sex on proximity with residents was not significant (when feeding, $\chi^2 = 0.2$, $df = 1$, $p = 0.669$; when resting, $\chi^2 = 1.9$, $df = 1$, $p = 0.163$) after controlling for kinship. Both models that excluded the interaction term were a better fit than the respective null models (when feeding, $\chi^2 = 7.4$, $df = 2$, $p = 0.024$; when resting, $\chi^2 = 8.6$, $df = 2$, $p = 0.014$). The two female classes did not differ significantly in the proportion of scans they spent in proximity with residents (when feeding, estimate ± SE = 0.28 ± 0.16, $p = 0.087$; when resting, estimate ± SE = − 0.22 ± 0.20, $p = 0.259$; Fig. 2; Table 3). However, both NFs and IFs were more often closely associated with RFs than with RMs (when feeding, estimate ± SE = − 0.38 ± 0.18, $p = 0.035$; when resting, estimate ± SE = − 0.54 ± 0.19, $p = 0.004$). Kinship had a significant effect on proximity, indicating that NFs were more often close to their mothers than to other individuals (when feeding, estimate ± SE = − 1.92 ± 0.26, $p < 0.001$; when resting, estimate ± SE = − 1.52 ± 0.19, $p < 0.001$).

Grooming interactions

After controlling for kinship, the interaction between focal female class and resident rank had no effect on the proportion of grooming (with RFs, $\chi^2 = 2.7$, $df = 2$, $p = 0.262$; with RMs, $\chi^2 = 0.3$, $df = 2$, $p = 0.874$). The model excluding this interaction term was a better fit than the null model for RFs ($\chi^2 = 15.7$, $df = 3$, $p = 0.001$),

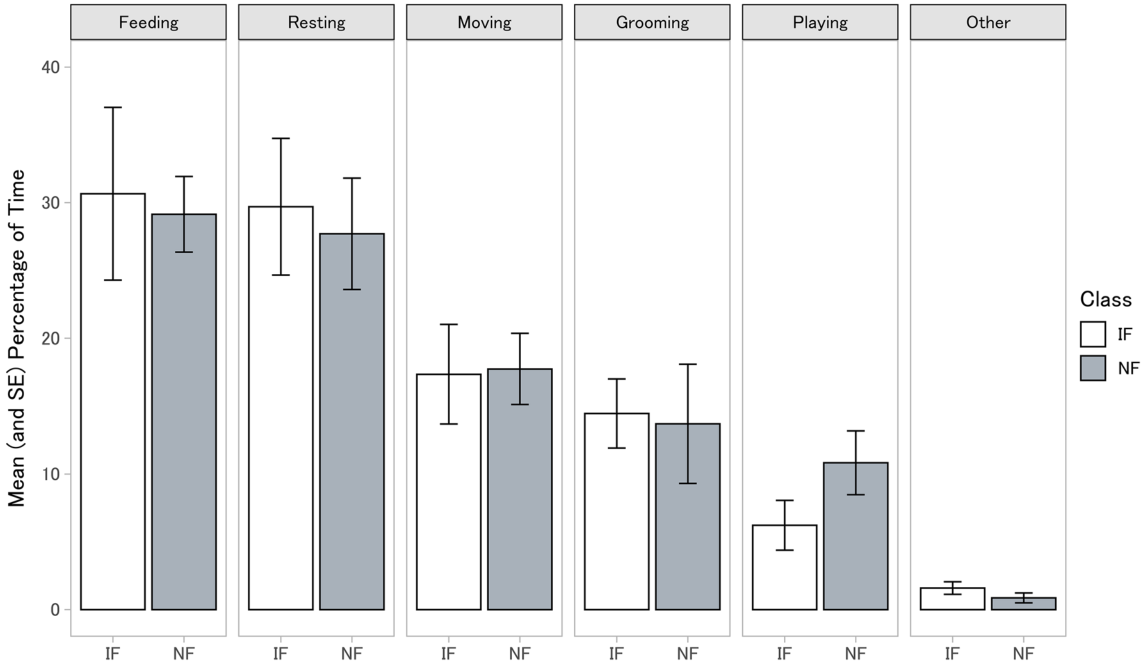

Fig. 1 Proportion of time that natal females (*NF*s) and immigrant females (*IF*s) participated in different activities during focal sampling

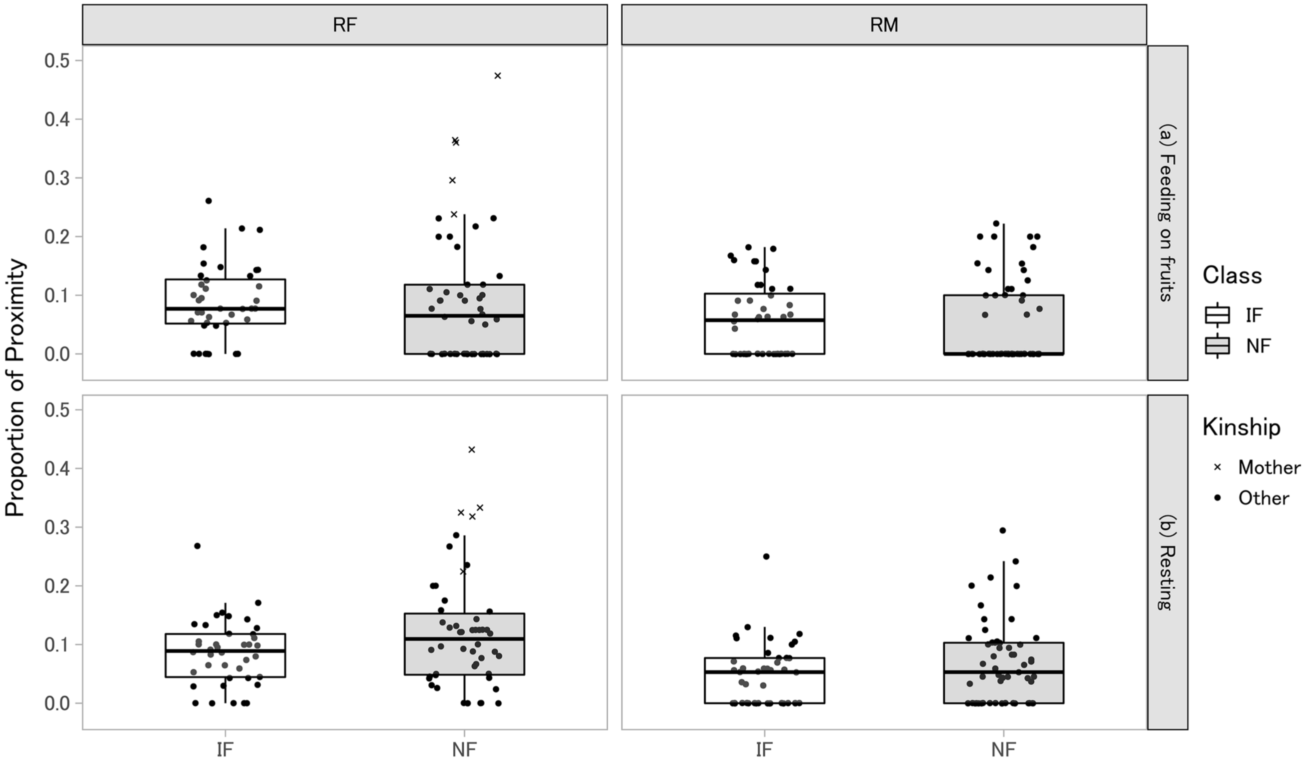

Fig. 2 Proportion of scan samples in which NFs and IFs were neighbors with each resident female (*RF*; *left panels*) and resident male (*RM*; *right panels*) when feeding on fruits (*upper panels*) or resting (*lower panels*). *Points* represent relationship/kinship between NF/IF and RF/RM, with *crosses* indicating mothers and *circles* indicating other relationships.

but not for RMs ($\chi^2 = 5.2$, $df = 3$, $p = 0.155$). NFs and IFs groomed high-ranking RFs more frequently than middle-ranking RFs (estimate ± SE = -0.66 ± 0.26, $p = 0.012$) and low-ranking RFs (estimate ± SE = -0.51 ± 0.25, $p = 0.043$; Fig. 3a; Table 4). Additionally, IFs groomed RFs more frequently than NFs did (estimate ± SE = 0.79 ± 0.29, $p = 0.007$), whereas NFs most often groomed their mothers (estimate ± SE = -2.83 ± 0.26, $p < 0.001$). Neither focal female class nor RM rank had a significant effect on the proportion of grooming between focal females and RMs (see Fig. 3b).

In the total duration of grooming integrations with all resident members, NFs had higher reciprocity indices than IFs (Mann–Whitney *U*-test: $W = 0$, $p < 0.019$; Table S2). All four IFs groomed high-ranking RFs for longer than they were reciprocally groomed. However, IFs were occasionally groomed by middle- and low-ranking RFs and RMs of all ranks for longer than they groomed in return. All five NFs spent more time being groomed by their mothers than grooming in return, while they groomed unrelated RFs and RMs for longer than they were reciprocally groomed.

Sexual interactions

The interaction between focal female class and resident rank had no significant interaction on the proportion of sexual interactions (with RFs, $\chi^2 = 1.3$, $df = 2$, $p = 0.534$; with RMs, $\chi^2 = 2.3$, $df = 2$, $p = 0.312$). When the interaction term was excluded, the refitted model for RFs did not differ from the null model ($\chi^2 = 3.9$, $df = 3$, $p = 0.278$), whereas the model for RMs was a better fit than the null model ($\chi^2 = 20.3$, $df = 3$, $p < 0.001$). Thus, neither focal female class nor RF rank had a significant effect on the proportion of GG rubbing interactions (see Fig. 4a). Additionally, IFs copulated with RMs more frequently than NFs did (estimate ± SE = 1.97 ± 0.41, $p < 0.001$; Fig. 4b; Table 4). NFs and IFs did not prefer to copulate with high-ranking RMs over middle-ranking RMs (estimate ± SE = 0.45 ± 0.44, $p = 0.302$) or low-ranking RMs (estimate ± SE = 0.48 ± 0.42, $p = 0.246$).

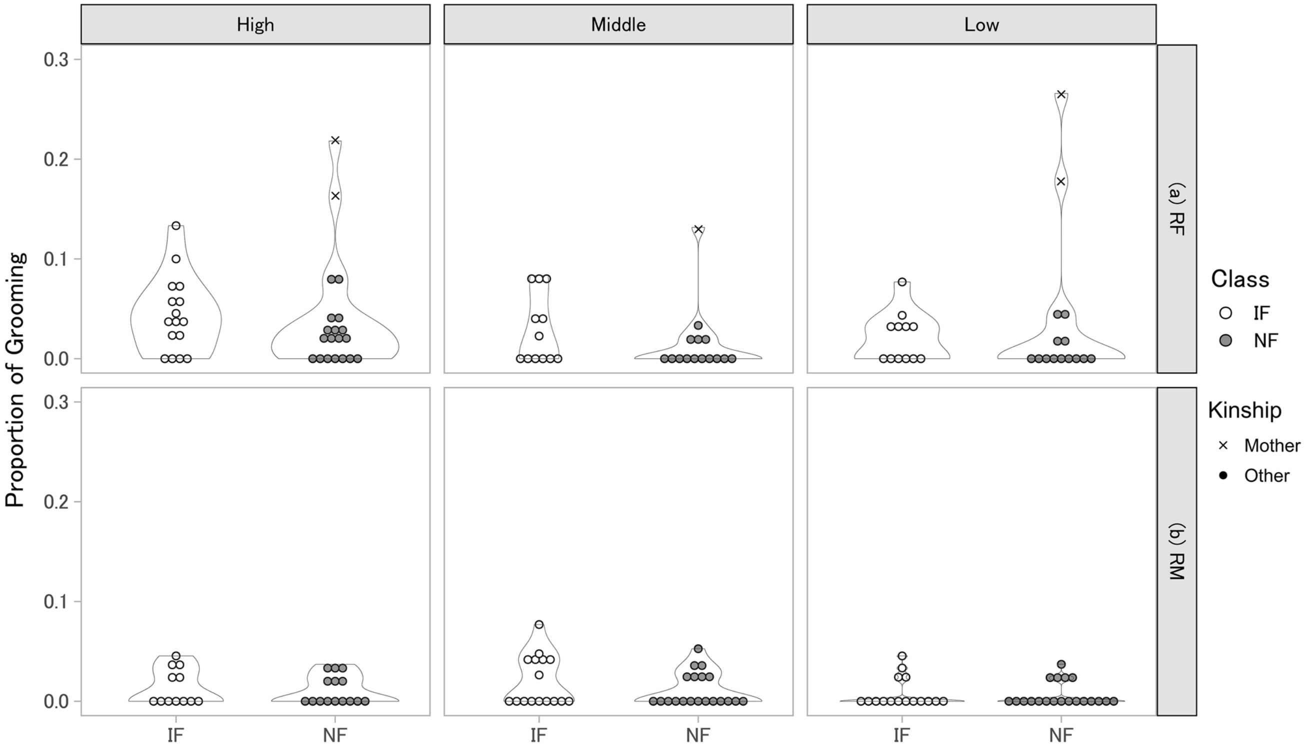

Fig. 3 Proportion of focal bouts that NFs and IFs spent in grooming interactions with each RF (*upper panels*) or RM (*lower panels*). The rank class of RFs/RMs is horizontally arranged [high ranking (*left*), middle ranking (*center*), and low ranking (*right*)]. *Points* represent relationship/kinship between NF/IF and RF/RM, with *crosses* indicating mothers and *circles* indicating other relationships.

Table 4 Results from models testing the effects of focal female class, resident rank, and kinship on the proportion of grooming interactions with each RF, and sexual interactions with each RM per focal bout, after non-significant interactions had been removed

Term	Estimate	SE	*Z*	*p*
Grooming interactions with RF				
(Intercept)	− 0.32	0.34	− 0.93	0.350
Class of focal female (NF vs. IF)	0.79	0.29	2.69	0.007*
Rank of RF (high vs. middle)	− 0.66	0.26	− 2.50	0.012*
Rank of RF (high vs. low)	− 0.51	0.25	− 2.02	0.043*
Kinship (mother vs. other)	− 2.83	0.26	− 10.90	< 0.001*
Sexual interactions with RM				
(Intercept)	− 3.93	0.35	− 11.28	< 0.001
Class of focal female (NF vs. IF)	1.97	0.41	4.80	< 0.001*
Rank of RM (high vs. middle)	0.45	0.44	1.03	0.302
Rank of RM (high vs. low)	0.48	0.42	1.16	0.246

For abbreviations, see Tables 1 and 2

* $p < 0.05$

Discussion

By comparing social interactions and spatial relationships between NFs and IFs, this study investigated how female bonobos developed social relationships after immigration into a new group. In line with previous research (Idani 1991), RFs did not focus aggression on IFs or isolate them spatially. Indeed, both NFs and IFs tended to be more closely associated with RFs than with RMs. Thus, female immigration into the E1 group did not appear to provoke overt competition with RFs. Contrary to our predictions that IFs would affiliate with high-ranking females more than NFs would, both classes preferentially groomed high-ranking RFs, and they also engaged in GG rubbing with RFs regardless of rank. Nonetheless, IFs spent more time than NFs grooming RFs despite being unrelated, whereas NFs tended to groom related RFs (mothers). This pattern implies that IFs, with no help from mothers, might have used grooming as a means of forming bonds with resident females in the new group. Our results partially support the hypothesis that immigrant female bonobos provide grooming services to higher-ranking females rather than to lower-ranking females. However, because NFs also preferred grooming high-ranking females, it is possible that all young female bonobos—regardless of immigration

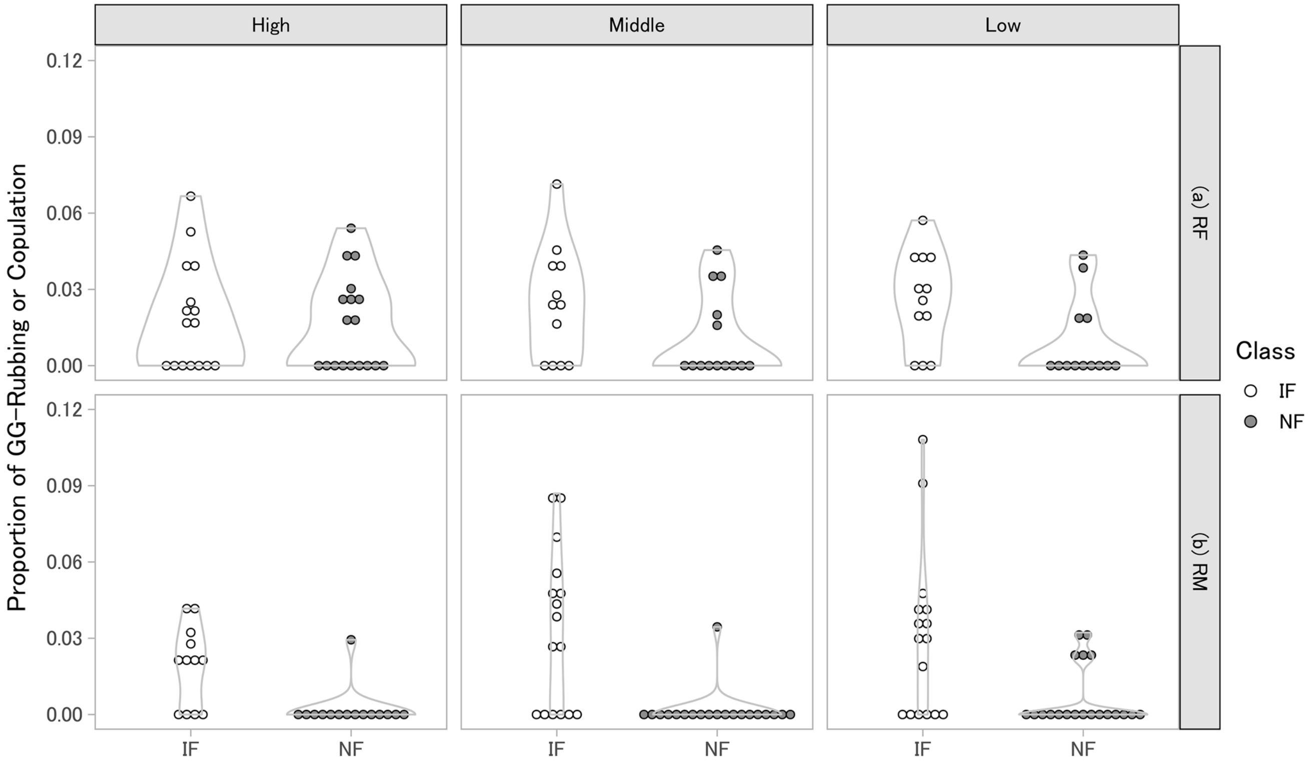

Fig. 4 Proportion of focal bouts that NFs and IFs spent in sexual interactions with each RF (*upper panels*) or RM (*lower panels*). The rank class of RFs/RMs is horizontally arranged [high ranking (*left*), middle ranking (*center*), and low ranking (*right*, respectively)]

status—target higher-ranking females as social partners to facilitate integration into the adult social group.

Mothers were the primary neighbors and grooming partners for NFs; compared with other group members, mothers devoted more time grooming NFs than being groomed. Separation from her mother is probably the largest change in the social environment of a female bonobo through dispersal. However, we found that NFs and IFs did not differ in the frequency of their close associations with unrelated RFs and RMs. Moreover, IFs still received grooming even though they had lower reciprocity indices than NFs overall. These data suggest that immigrant female bonobos may incur a smaller social disadvantage associated with the unavailability of their mothers than immigrant female chimpanzees, likely due to between-species differences in female intrasexual relationships. First, from 3–4 years of age, female bonobos begin to exhibit weaker spatial relationships with their mothers than female chimpanzees (Lee et al. 2020). In general, female chimpanzees maintain strong social bonds with their mothers when they remain in their natal group (Kahlenberg et al. 2008b; Langergraber et al. 2009), and maternal presence/rank enhances their reproductive rates (Foerster et al. 2015; Walker et al. 2018), whereas neither is the case for female bonobos to the best of our knowledge (cf. Moscovice et al. 2017). Likely due to a fitness advantage based on feeding competition, female chimpanzees with higher-ranking mothers are more likely to remain in their natal group than those with lower-ranking mothers (Walker and Pusey 2020). Given these characteristics, mothers may be less important for female bonobos than for female chimpanzees.

Our comparisons showed that NFs and IFs were exposed to a similar frequency of aggression from RFs and had similar spatial relationships during feeding. We did not find any evidence of RFs preventing IFs from using the same food patch. The higher tolerance of female bonobos to non-kin compared with female chimpanzees might be because food patches tend to be more widely distributed and abundant in bonobo habitats than in chimpanzee habitats (Badrian and Badrian 1984; White and Wrangham 1988). Bonobos may also experience less interspecific conflict over terrestrial food resources than chimpanzees because, unlike the latter, their ranges do not overlap with those of gorillas (Hare et al. 2012; Malenky and Wrangham 1994). However, low-ranking female bonobos still have a slightly lower feeding efficiency than higher-ranking females, possibly because of a trade-off between high gregariousness and feeding opportunity (Nurmi et al. 2018). Female bonobos are particularly prosocial toward outgroup members (Idani 1990; Tan and Hare 2013; Tan et al. 2017; Tokuyama et al. 2019). Bonobo groups frequently encounter each other and may commingle, especially during periods of high fruit abundance (Sakamaki et al. 2018; Lucchesi et al. 2020). Further research is required to clarify the factors behind bonobo prosociality.

Unexpectedly, RMs were more aggressive toward IFs than toward NFs, although male aggression never resulted in serious injury. We do not have a clear explanation regarding the function of male aggression toward IFs. Male bonobos are unlikely to harass IFs as a form of sexual coercion, given that such aggression rarely leads to forced copulation (Surbeck and Hohmann 2013), in contrast to male chimpanzees (Muller et al. 2007, 2011). Instead, RMs appeared to exhibit aggression toward IFs, who were still submissive to them, to reinforce their dominant status even though female bonobos will outrank many males as they age (Furuichi 1997; Tokuyama and Furuichi 2016; this study). We also observed three cases of RFs intervening in male aggression towards IFs. These observations are consistent with those of a previous study, suggesting that a female coalition countering male harassment may benefit young females (Tokuyama and Furuichi 2016). The social role of resident female bonobos is somewhat similar to that of male chimpanzees in protecting immigrant females.

The biological market theory proposes that animals mutually exchange beneficial interactions as a "currency" (Noë and Hammerstein 1995). For instance, lower-ranking individuals groom higher-ranking individuals in return for social support provided by the latter [e.g., vervet monkeys (*Cercopithecus aethiops*) (Seyfarth and Cheney 1984); chacma baboons (*Papio ursinus*) (Barrett et al. 1999); tufted capuchin monkeys (*Cebus apella*) (Tiddi et al. 2012); chimpanzees (Kutsukake and Clutton-Brock 2010)]. Here, our results are partially in line with the existing hypothesis of older female bonobos being important partners that help immigrant females integrate into a new group (Idani 1991). IFs groomed high-ranking RFs more than they did middle- and low-ranking RFs. They also spent more time grooming high-ranking RFs than being groomed by those RFs, but had no significant preference for grooming high-ranking RMs. Because male dominance rank in bonobos changes over time while female dominance rank remains comparatively stable (Furuichi 1997), it may be more efficient for immigrant females to invest in grooming high-ranking females rather than high-ranking males. However, similar to IFs, NFs tended to focus on grooming high-ranking RFs, even though their mothers were their primary grooming partners.

As previously stated, we cannot rule out the possibility that pubertal female bonobos generally have rank/age-related preferences for grooming partners, regardless of immigration events. To determine whether immigration is the sole cause would require separating the immigration event from the developmental process, but this was out of our control in the field. Indeed, such a social preference among immature individuals has been reported in multiple primate species with female philopatry [e.g., vervet monkeys (*Chlorocebus pygerythrus*) (Fairbanks 1993); hanuman langurs (*Presbytis entellus*) (Nikolei and Borries 1997); blue monkeys (*Cercopithecus mitis*) (Cords et al. 2010)]. Further studies should therefore investigate whether female bonobos that remain in the natal group are similar to immigrant females in spending more time grooming unrelated females, especially higher-ranking ones.

GG rubbing among female bonobos regulates social tension and facilitates cooperation (Kuroda 1980; Hohmann et al. 2009; Moscovice et al. 2019). In contrast with a previous report from the same field site (Idani 1991), we observed that IFs engaged in GG rubbing interactions with a wide range of RFs, regardless of rank. This between-study difference may be associated with the presence or absence of provisioning. Provisioned food resources are usually clumped in a small place, potentially strengthening feeding competition and prompting immigrant females to focus GG rubbing on high-ranking old females. Without provisioning, GG rubbing is likely to be more opportunistic, occurring whenever conflicts require mitigation. We also observed that NFs engaged in GG rubbing with RFs at similar frequencies as IFs did, even though their sexual swellings were still immature. This observation is in line with previous research showing that GG rubbing develops during the juvenile stage before dispersal (Hashimoto 1997). This socio-sexual behavior may benefit female bonobos in terms of forming bonds with unrelated females during immigration.

Adolescent female bonobos typically have a longer period of sexual swellings and lower chance of fertility than parous females (Furuichi 1987; Ryu et al. 2015), similar to female chimpanzees (Wallis 1992; Deschner and Boesch 2007). Prolonged sexual swellings of adolescent female chimpanzees may attract resident males for a long period during immigration (Kahlenberg et al. 2008a). In our study, IFs had more prominent sexual swellings than NFs, and correspondingly, copulated more frequently with RMs than NFs did. However, NFs and IFs had similar frequencies of proximity to RMs, indicating that differences in sexual receptivity do not strongly affect spatial relationships. In bonobo society, higher-ranking males have more opportunities to copulate with fertile females than lower-ranking males (Surbeck et al. 2011). Moreover, we observed that IFs copulated with RMs of any rank. Therefore, similar to chimpanzees (Muller and Wrangham 2004; Sobolewski et al. 2013), male bonobos may compete with each other for adolescent females less frequently than for adult females.

In summary, our data suggested that female bonobos groomed high-ranking old females to facilitate successful integration into their new group, in line with a previous hypothesis (Idani 1991). We also provided evidence that immigrant female bonobos were tolerated by resident females and did not require male protection, in contrast to female chimpanzees. Nonetheless, this study had several limitations that affected our ability to draw conclusions. First, our sample sizes were small. Second, we could not control for age effects on the behavior of female bonobos during development. Moreover, our work leaves unanswered the intriguing question of why resident females tolerate immigrant females. The fact that immigrant females groom high-ranking old females may partially explain this tolerance. However, to fully understand the mutual benefits in social relationships between immigrant and resident female bonobos, more extensive behavioral sampling of their social interactions should be performed in future studies.

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Declarations

Conflict of interest The authors declare no competing interests.

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